

The effects of aircraft noise on avian communities and communication

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Abstract: Noise generated by low-altitude aircraft movements reaches levels higher than many other anthropogenic noise sources. How birds respond to these acute noise levels is, to date, poorly understood. This thesis provides some of the first data on how noise generated by aircraft affects avian communities and communication.

Firstly, point counts conducted around Manchester airport show there is no effect of increasing noise levels on beta diversity. In addition, results show the density and abundance of the two most abundant species and the number of detections for the five most common species was also unaffected.

Secondly, comparisons of the songs of the abundant chiffchaff reveal that airport birds use lower frequency songs than control birds. This finding was replicated in two countries. Additionally, the songs of airport birds in the UK are longer and slower than control birds. These findings may be explained by birds that are found close to airports are suffering from Noise Induced Hearing Loss (NIHL). This was supported when comparing the responses of airport and control chiffchaffs to territorial songs; airport chiffchaffs were more aggressive, attacking the speaker 5 times more than control birds. An explanation for this is that as an artefact of NIHL, airport birds perceive songs differently to those in the control site.

Finally, physiological stress induced by aircraft noise was investigated. There were no differences in corticosterone levels, a proxy for measuring stress levels, between 11-day old blue tit chicks exposed to noise treatments and control chicks. These findings suggest that pre-fledging blue tit chicks do not perceive anthropogenic noise as an environmental stressor.

Whilst the work in this thesis does not detect an effect of aircraft noise on the species community or corticosterone levels, it does provide evidence consistent with the loss of hearing in birds as a consequence of anthropogenic noise exposure.

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Chapter 1- Introduction

Abstract- Anthropogenic noise has negative impacts on wildlife at an individual and community level. Increases in road, sea and air travel mean that noise affects life in even the most remote locations. Whilst the understanding of the impacts of road and urban noise grows, little is known about how aircraft noise affects wildlife. Unlike that generated by roads and industry, aircraft noise is typically much louder and noise events are intermittent and frequent. Here the literature is reviewed on how animals are able to adapt to life in a noisy environment. Noise has negative effects on biodiversity, reducing species abundance and modifying community assemblages. Noise also impairs communication through masking. Whilst some species are able to modify signals to improve signal to noise ratio, this can affect the integrity of the signal and the information encoded within. Finally, noise affects physiology by causing hearing loss, reducing reproductive success and lowering immune responses. With airport expansion figuring in political debate in the UK and worldwide, it is timely to highlight the impacts of aircraft noise on wildlife.

1.1 Anthropogenic noise research

Noise generated by growing human populations and its effects on wildlife has attracted much attention from researchers in the past decade. Noise can affect biodiversity by changing communities through loss of species, affecting survival rates or by affecting the way species communicate and reproduce. The effects of noise have been studied in a wide range of animals as well as humans and there are many parallels in the type of response (Kight & Swaddle 2011).

Noise can negatively affect biodiversity by reducing the number of species found in otherwise suitable habitats (Goodwin & Shriver 2011). The impact of noise can also affect species compositions by altering age demographics (Mcclure et al. 2016). Noise reduces fitness through affecting communication (e.g. signal masking) and influencing physiology (e.g. increased stress, lower immune response)(Kight et al. 2012).

Noise can be defined as any sound that inhibits the ability to discriminate between signals or discriminate signals from background disturbance (Wiley & Richards 1978). Noise impedes the transmission of information encoded in a signal by reducing the signal-to-noise ratio (Lengagne 2008). If the signal to noise ratio is too low, or if the amplitude of the noise exceeds the amplitude of the signal, the signal is masked.

1.2 Sources of anthropogenic noise

Abiotic noise, generated from wind, rain and waves can affect acoustic communication. Rainfall for example can significantly reduce the propagation distance of a signal in broadleaf woodland (Lengagne & Slater 2002). Natural abiotic noise can be more detrimental to communication than anthropogenic noise. For instance, greater mouse-eared bat (*Myotis myotis*) show reduced foraging efficiency in the presence of both road and natural noise, however natural noise shows a greater repelling effect than

road noise (Schaub et al. 2008). Increasingly for many organisms, the dominant background noise is not generated by natural sources. Anthropogenic noise, is typically louder, more frequent and more common than abiotic noise (references in: Kight & Swaddle 2011). The most common source of anthropogenic noise is that generated by road traffic (Barber et al. 2010). Other major sources include industry, construction work and recreational activities (Slabbekoorn 2013). One of the reasons that anthropogenic noise is so disruptive is because it can travel long distances before it attenuates. Anthropogenic noise contains most of its energy in the lower part of the frequency spectrum (Warren et al. 2006) and low frequency sound waves are less affected by attenuation from atmospheric conditions or structural objects than high frequency sounds. The long wavelengths of low frequency sound are more robust than high frequency sounds to the effects of energy absorption and refraction, two main causes of noise decay (reviewed in Berglund, Hassmén, & Job, 1996). As a result, low frequency sounds can cross large distances with little energy loss and can still be detected far from the source (Reijnen et al. 1995). Indeed, negative effects of vehicle noise can be found hundreds of meters from roads (reviewed in Forman, Reineking, & Hersperger, 2002).

1.3 How loud is too loud?

Despite the known health effects of noise, no current universal noise level that qualifies noise as pollution exists. EU guidelines suggest that for humans sound pressure levels between 50-55dB(A) are loud enough to cause medium to severe annoyance (WHO 1999). The effects of noise on hearing depends on two main factors (1) the noise level (or amplitude) and (2) the duration of exposure (Eggermont 2016). In humans noise levels exceeding 105dB(A) for greater than 1 hour are considered traumatic and lead to permanent loss of hearing, however the longer the duration of exposure, the lower the noise levels required to cause hearing loss (Eggermont 2016).

The level of noise will vary depending on the source, the frequency of the noise and the distance from the source as well as the surrounding habitat type (Dooling & Popper 2007). Signals will propagate further in open habitats than closed habitats (Ronald et al. 2012). Noise levels that affect an individual will depend on its auditory capabilities and sensitivity. Tawny owls (*Strix aluco*), reduce the number of important vocalisations including territory and courtship calls at noise levels of 49.8 dB(A) (Lengagne & Slater 2002). At lower amplitudes, effects of noise are typically limited to signal masking and changes in signalling behaviour or signal structure (Dooling & Popper 2007) but as the level of the noise increases the effects become stronger. Chickens (*Gallus domesticus*) and serins (*Serinus serinus*) respond to moderate noise exposure by either increasing the rate of calling or the proportion of time spent singing (Brumm et al. 2009; Díaz et al. 2011), presumably to increase the chance of the signal being detected. However, when the noise exceeds an amplitude threshold of around 70 dB (A), the rate and duration of signalling returns back to as if there was no noise. This may be because many organisms require self-auditory feedback and if noise levels are high, an individual may not be able to hear enough of the signal it is producing.

Where noise levels are extremely high, there can also be effects of acoustic overexposure that can result in the loss of hearing. Noise levels affect hearing by shifting auditory detection thresholds. Auditory threshold shifts mean that either whole signals, or parts of a signal, need to be louder in order to be detected by the receiver. In some cases damage to or over stimulation of the hair cells may mean that the signaller is unable to hear any part of a signal. These detections shifts can either be temporary (temporary threshold shifts (TTS)) or permanent (PTS) depending on the duration, severity and frequency of the acoustic overexposure (Dooling & Popper 2007). In cases of progressive TTS, that is where the physical degradation and subsequent loss of the hair cells takes

place over a period of time, high frequency sounds are typically the first to be affected (Holme & Steel 2004).

Birds, in contrast to mammals are able to recover inner hair cells even if they are completely lost after acoustic trauma (Dooling et al. 2000). This makes them ideal subjects for studying the effects of hearing loss on signal perception as individuals can be tested before, during and after the hearing cells have recovered. Indeed, experiments involving several surgically deafened bird species have shown changes in singing behaviour during periods of threshold shifts (partial or complete deafness). Singing behaviour returns back to normal once the hair cells have recovered (Watanabe & Sakaguchi 2010; Watanabe et al. 2007; Brittan-Powell & Dooling 2004).

Detection threshold shifts can result from exposure to extremely high noise levels. Noise induced hearing loss (NIHL) occurs when disruption by noise causes inner and outer hair cell loss and auditory nerve degeneration. Damage to the hair cells can be a result of exposure to a single impulse noise of a very high level, or as a result of frequent exposure to lower noise levels. NIHL has been studied in humans, mammals (Gannouni et al. 2015) fish (Smith et al. 2004) and birds (Marler & Konishi 1973) and the noise levels and periods of noise exposure that result in NIHL vary between species. Rats show signs of hearing loss when exposed to amplitudes of 88dB while fish show auditory threshold shifts after 10 minutes exposure to noise levels of 100dB(A) and birds show threshold shifts after exposure to amplitudes of 75dB(A)(Dooling & Popper 2007)

1.4 Aircraft noise

The impact of aircraft on wildlife has received limited research attention. The sound signature of aircraft noise is similar to that of terrestrial

vehicles and both contain most of the power in the lower end of the frequency spectrum (Fig. 1). Aircraft noise does however have a wider bandwidth with more energy present at both higher and lower frequencies.

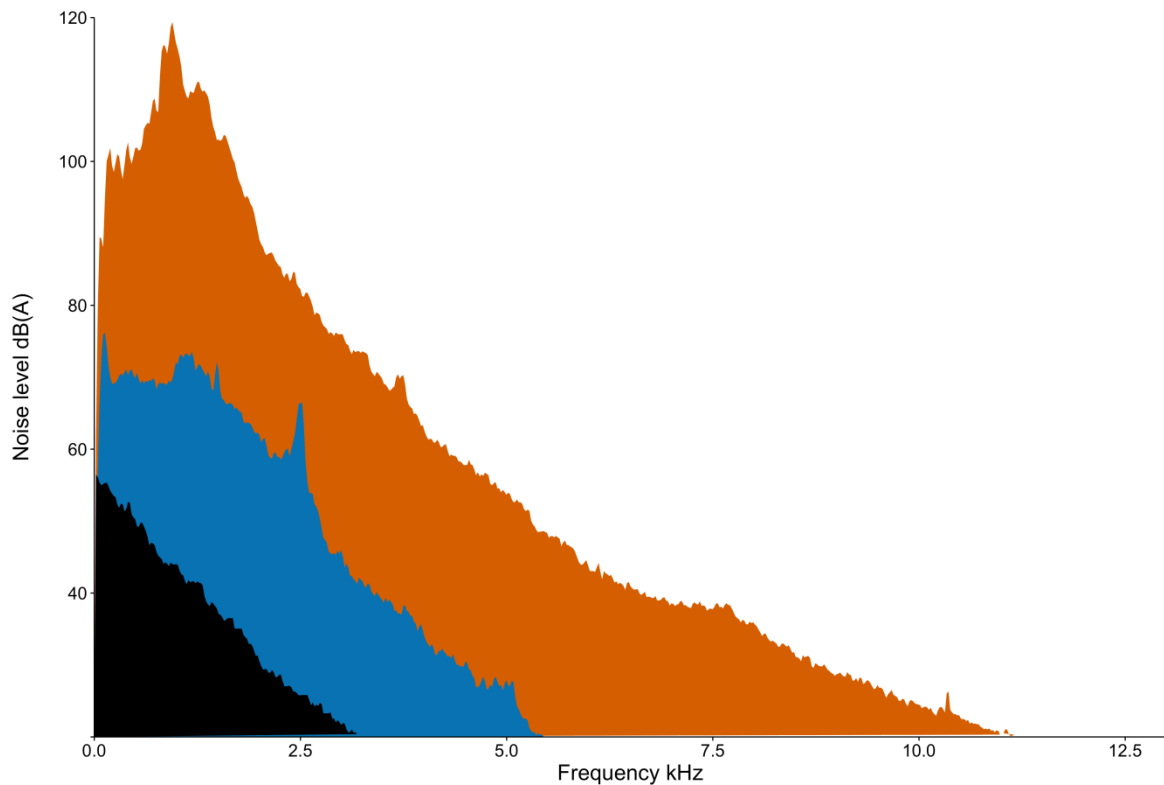


Figure 1.1- Power spectrum showing the frequency range for an aircraft built in 2015, (red area), road noise (blue area) and woodland noise. Frequency and amplitude ranges are derived from recordings taken close to Manchester airport and a busy motorway.

Aircraft noise deviates from most anthropogenic noise sources in temporal and amplitude patterns. Road and urban noise are both typically constant, whereas aircraft noise consists of infrequent bouts of acoustic events separated by periods of relative quiet. Despite the development of quieter engines even the most modern of aircraft produce noise levels much higher than those generated from other anthropogenic sources (fig 1.1).

Aircraft noise also differs from other anthropogenic noise profiles in how the noise propagates from the source (Egan 2007). The noise generated by

roads is expected to be linear, that is the noise is at its highest levels along the length of the road gradually decaying further away. Aircraft noise however has a radial distribution where the noise produced by the engines emanates away from the aircraft to all directions. As the aircraft gains height, the noise levels drop and the spread of the noise increases.

Previous research on the impacts of aircraft noise mainly focused on its effects on humans. Exposure to noise has been linked to secondary health issues such as tinnitus, hypertension, cardiovascular problems and increased risk of stroke (Basner et al. 2014). However, airport policies ensure that due to the negative effect of aircraft noise on human health (Basner et al. 2014) the flight paths are situated to minimise disturbance from aircraft noise on humans. This typically means that aircraft are directed over uninhabited or sparsely populated areas, and therefore increases the exposure of aircraft noise to wildlife.

Whilst data are limited for how this affects wildlife, aircraft disturbance induces behavioural or physiological responses in several species of bird. These responses include increases in vigilance or alert behaviours as seen in crested terns (*Sterna bergii*) (Brown 1990), harlequin ducks (*Histrionicus histrionicus*) (Goudie 2006), Canadian geese (*Branta canadensis taverneri*) (Ward & Stehn 1999) and Great tits (*Parus major*) (Klett-Mingo et al. 2016). Aircraft noise also leads to increases in aggression in herring gulls (*Larus argentatus*) (Burger 1981) elevated startle responses in wood ducks (*Aix sponsa*) and black ducks (*Anas rubripes*) (Conomy et al. 1998) and increases in flight responses and nest attendance in peregrine falcons (*Falco peregrinus*) (Ellis et al. 1991; Palmer et al. 2003). Aircraft noise also reduces reproductive success in Mexican spotted owls (*Strix occidentalis lucida*) (Delaney et al. 1999).

There are also data that have failed to show an effect of aircraft disturbance on reproduction. No decrease in reproductive success was seen in peregrine falcons (Palmer et al. 2003) or ospreys (*Pandion*

haliaetus)(Trimper & Standen 1998) living near military airbases. In addition, several studies report rapid habituation to aircraft noise. This however seems to be highly species specific. Whilst black ducks show less response to aircraft movements after 17 days exposure, the closely related wood duck did not show signs of habituation (Conomy et al. 1998). It is important to note that many of these studies have focused on the effects of military aircraft disturbance where few aircraft movements take place per day. However noise generated by commercial aircraft alters the timing of birdsong (Gil et al. 2014; Dominoni et al. 2016).

Whilst birds exposed to aircraft noise display negative behavioural responses (i.e. increase in startle behaviours), there is currently no information on how aircraft noise affects species compositions or if aircraft noise is physiologically stressful. Two studies have addressed how birds shift the timings of their songs to reduce overlap with aircraft noise (Dominoni et al. 2016; Gil et al. 2014), however none have yet explored if birds modify spectral parameters to improve signal transmission. The next section of this thesis explores the way birds respond to moderate noise. The findings may assist in understanding the mechanisms and strategies that enable to adapt to life around airports.

1.5 Response to noise

Ecological effects of noise

Anthropogenic noise can shape communities by reducing the total number of species present at a specific location (alpha diversity), and the difference in species composition between sites (beta diversity) (Proppe et al. 2013) and modify community structure (Habib et al. 2006; McClure et al. 2016). Reduction in alpha diversity be due to the exclusion of some species for example if noise prevents effective communication (Blickley et al. 2012). Diversity may also be reduced if noise prevents feeding or reduces foraging efficiency. Greater mouse-eared bats (*Myotis myotis*) stop feeding in noisy areas and subsequently move to areas with lower

noise levels (Schaub et al. 2008). The exclusion of species may have cascade effects resulting in alterations to landscape ecology, especially if species that act as seed dispersal units are absent from noisy areas (Francis et al. 2009). Reductions in species diversity where noise is thought to be the main contributor can be found in primates and ungulates (Laurance et al. 2008), frogs (Herrera-Montes & Aide 2011) and birds (Dooling & Popper 2007)

Impact of noise on communication

Whilst mechanisms exist to allow signal propagation in a naturally noisy environment, anthropogenic noise is driving the adaption of species in unnaturally noisy environments (Bermúdez-Cuamatzin & Ríos-Chelén 2009; Pohl et al. 2012; Halfwerk & Slabbekoorn 2009; Ríos-Chelén et al. 2012; Patricelli & Blickley 2006a). Anthropogenic noise is typically loud and low in frequency (Slabbekoorn & Ripmeester 2008; Bermúdez-Cuamatzin & Ríos-Chelén 2009) and can mask signals used by animals (Brumm, 2004; Goodwin & Podos, 2013; Lohr, Wright, & Dooling, 2003; Shier, Lea, & Owen, 2012). For communication to be effective the signal-to-noise (SNR) ratio needs to be sufficiently high at the receiver end for information transfer (Warren et al. 2006). In response to noise, signallers can deploy a number of strategies to increase SNR.

Amplitude adjustment

One strategy to increase the signal to noise ratio is to increase the amplitude of the signal. By increasing the amplitude to be louder than that of the noise, the signal is released from masking. This is known as the Lombard effect (Brumm & Zollinger 2011). First observed in humans, the Lombard effect is common throughout the animal kingdom and has been found in every bird (Brumm & Zollinger 2011) and mammal species (Hotchkin & Parks 2013) tested. The use of amplitude increase to counteract background noise has not been detected in anurans. This has

led to suggestions that this strategy has either evolved as a synapomorphy between birds and mammals and has been derived from a common ancestor, or that the Lombard effect has evolved independently in the two groups (Brumm & Zollinger 2011).

Frequency modulation

A second commonly found adaptation to enable masking release is frequency modulation. Spectral masking occurs when the background noise and the signal noise share the same spectral frequency. Frequency modulation is the shifting of the spectral frequency of the signal so that it no longer overlaps with the noise. Bird species found around rivers often use high frequency calls, presumably to combat the low frequency masking effects generated by water movement (Dubois & Martens 1984). Anthropogenic noise can also drive frequency shifts (Slabbekoorn & den Boer-Visser 2006). Urban blackbirds (*Turdus merula*) use higher frequency songs than their rural conspecifics. This shift to higher frequency songs can influence intraspecific interactions with different responses to songs from rural and urban males (Ripmeester et al. 2010). Whilst increasing song frequency may be explained as an adjustment to improve signal to noise ratios they may also result from amplitude adjustment. The maximum frequency of nightingale (*Luscinia megarhynchos*) songs show a positive correlation with amplitude (Brumm 2010). Birds that sing louder use songs with higher maximum frequencies. However, there are cases where singing at higher amplitudes leads to lower minimum frequencies (Zollinger et al. 2012). This has led to the question if frequency modulation is an artefact of the Lombard effect, or whether it is an independent strategy to improve signal detection. This topic has stirred much debate within the literature (Zollinger et al. 2012; Cardoso & Atwell 2012; Halfwerk et al. 2012).

Temporal modulation

Signallers can improve the chance of detection by altering the frequency or amplitude of a signal. However, during very high amplitude noise events masking release may not be achieved using these strategies. The levels of noise generated by aircraft taking off may result in the saturation of the auditory filters resulting in the total loss of signal detection (Complete masking; (Moore 2012)). Comodulation masking release (CMR), signalling during periods of low amplitude background noise, can aid signal detection. Humans take advantage of fluctuations in amplitude to improve vocal signal detection (Hall et al. 1984). Non-human primates also adjust the timing of signals to periods of quiet (Egnor et al. 2007). Nightingales (*Luscinia megarhynchos*) time the onset of their songs to coincide with quiet periods (Brumm 2006b). Birds found close to airports shift songs to earlier on the day, presumably to reduce the impacts of masking by aircraft noise (Gil et al. 2014)

Bird song is at its most intense in the early part of the morning when environmental conditions for signal propagation are at the optimum level (Brown & Handford, 2003). During this period multiple species will be attempting to communicate, and birds can adjust their singing times to reduce overlap with other species to avoid signal masking (Brumm 2006b). In urban centres and particularly close to major roads, peak noise levels generated by road traffic during rush hour, can coincide with peak calling times for birds (Warren et al. 2006). Road noise modifies the timing of the onset of singing in spotless starlings (*Sturnus unicolor*) and house sparrows (*Passer domesticus*) experimentally exposed to noise (Arroyo-Solís et al. 2013). Urban robins (*Erithacus rubecula*) avoid signal interference by singing at night when ambient noise levels are lower (Fuller et al. 2007).

In addition to shifting the timing of signals, sending the same signal more frequently can also improve the opportunity for signal detection. In

humans, repeating a signal in a noisy environment improves the rate of detection (Fastl 1993). Increased serial redundancy in acoustically noisy environments has also been detected in birds (Brumm & Slater 2006) and in visually noisy habitats in reptiles (Ord et al. 2007). This suggests that, as with humans, increasing the delivery rate of a signal is an effective way of maintaining communication in noisy conditions. There may however be limitations to increasing signalling redundancy. Signalling more often results in a higher proportion of time spent singing (Díaz et al. 2011), time which may otherwise be used for other important behaviours such as foraging or courtship. In addition, for many species, the rate at which a signal is given contains information. This information may inform the receiver of the signaller's level of motivation (Ręk & Osiejuk 2010). In these instances, the use of increasing signal redundancy may compromise the information content of the signal (Brumm & Slabbekoorn 2005). Increasing the number of times a signal is delivered may only be beneficial in conditions where the amplitude of the masking noise is relatively low. (Brumm et al., 2009; Díaz et al., 2011).

Effects of noise on cognition, health and reproduction

Noise can also impact health, tolerance levels and affect concentration (reviewed in Pepper et al. 2003b; Stansfeld 2003). Glucocorticoids are hormones commonly used as a measure for stress response (references in (Blickley et al. 2012)). Laboratory and field based experiments have shown increased endocrine levels in children exposed to intermittent noise (Stansfeld 2003). A similar effect has also been detected in Greater-sage Grouse (*Centrocercus urophasianus*) (Blickley et al. 2012).

Noise contributes to a reduction in cognitive ability. Exposure to noise negatively influences concentration, problem solving and can reduce academic ability in children (Clark & Stansfeld 2007). Similar cognitive effects can be found in non-human mammals and invertebrates. Mice exposed to loud noise take longer to successfully complete problem

solving tasks and show poor short term memory retention (Cheng et al. 2011; Naff et al. 2007).

An explanation for reduced cognitive function is that noise distracts by relocation the individual's attention to the noise (Chan & Giraldo-Perez 2010). Hermit crabs (*Coenobita clypeatus*) exposed to simulated boat noise respond slower to a visual stimulus (Chan & Giraldo-Perez 2010). Noise may also lead to an increase, or perceived increase in predation risk. Increased vigilance has been detected in mammals and birds exposed to noise (Quinn et al. 2006; Owens et al. 2012; Chan & Giraldo-Perez 2010) (Rabin et al. 2006). Distraction from noise has also been reported to reduce foraging efficiency in bats (Siemers & Schaub 2011), fish (Purser & Radford 2011) and birds (Quinn et al. 2006).

Effects of noise on reproductive success have been reported in humans and animals (reviewed in Kight & Swaddle, 2011). This can be through an increase in the risk of premature birth as seen in humans (Etzel et al. 1997). Exposure to anthropogenic noise during embryonic development increases physical deformities in developing New Zealand scallops (*Pecten novaezelandiae*) (de Soto et al. 2013), increases mortality in developing chicks and reduces egg production in great tits (*Parus major*) (Halfwerk, Holleman, et al. 2011). Noise also weakens pair bonding in Zebra finches (*Taeniopygia guttata*) (Swaddle & Page 2007) and reduces pairing success in ovenbirds (*Seiurus aurocapilla*) (Habib et al. 2006).

1.6 Conclusion

As the human population increases so too does the demand for urban areas. Understanding the impact of urbanisation and noise levels on wildlife will therefore become more pertinent. Creating protected areas close to significant noise sources may not fulfil conservation aims if noise impacts are not known or considered. Birds and humans often benefit from the same or similar noise mitigation methods (Slabbekoorn &

Ripmeester 2008). Understanding how species respond to different types of noise pollution can aid mitigation methods and ensure appropriate action is taken for affected areas. Despite the increasing number of studies on noise impact on animals there are few that manage to isolate the impact of sound from confounding factors (Radford & Morley 2012). Much of the definitive data on noise impacts are provided by laboratory-based research with limited relevance to natural situations. One of the primary difficulties in field-based experiments is separating the effects of noise from other components of anthropogenic disturbance. Recent studies have however gone some way in isolating the effects of noise (McClure et al. 2013, McClure et al. 2015, McClure et al. 2016)). A 'phantom road' using a network of speakers that produced traffic noise resulted in a decline of bird species, changes in age demographics and reductions in body mass on days where road noise was played compared to control sites. Future anthropogenic noise research using similar techniques should ensure claims regarding the negative effects of noise on fitness are indeed because of noise and not due to confounding factors.

Given the limited data available on the effects of aircraft noise, this PhD thesis aims to identify if airports affect birds from four different perspectives. These perspectives draw on findings from anthropogenic noise studies and aim to identify if the effects of aircraft noise are similar to those caused by well-researched anthropogenic noise sources, such as road noise.

Firstly, to address how aircraft noise affects bird communities, the diversity and density of the bird community was assessed around an airport (objective 1). Secondly, the impact of aircraft noise on vocal communication was explored. This examined the effects of noise disturbance on communication from the position of the signaller (objective 2) and receiver (objective 3). Finally, to identify if living close

to an airport causes stress in birds as it does in humans, the physiological effect of exposure to aircraft noise is explored (objective 4).

1.7 Study site

For objectives 1, 2 & 4 Manchester international airport was used as a case study. In 2016 Manchester airport was the fourth busiest in the UK servicing 25 million passengers, this represents a 9% increase from 2015 and has increased from 18 million passengers in 2010. The number of freight aircraft movements is also predicted to rise as route networks are expanding to include new airports (MAG environment policy 2016). During peaks times an aircraft movement occurs every 2 minutes. Whilst the overall site covers some 625 hectares, 350 hectares of this is non-operational and consists of several habitat types (MAG environment policy 2000). The Manchester Airport Group is committed to sustainable air travel and the area around the runways has seen the airport invest heavily in environmental mitigation. Since 1997 the airport has created 25 hectares of wildflower grassland and 50 hectares of woodland and scrub (MAG environment policy 2000).

As a control site a large nature reserve (Woolston Eyes) was identified approximately 20km away from the airport. The nature reserve covers approximately 300 hectares and the habitat closely resembles that found around the airport. The site is a disused dock that serviced several large mills along the Manchester ship canal during the 19th century. There are large patches of scrub, grassland and small patches of woodland.

1.8 Study species

The selection process for potential study species for objectives 2&3 was conducted prior to any data being collected. Two main requirements were (1) that the species was present in large numbers at both the airport and control site to ensure a large enough sample size, and (2) that previous work investigating the effects of noise had been performed on the species.

To address requirement 1, the airport was visited on a regular basis to assess which species were present and to estimate the abundances. Power analysis suggested that for objective 2 (see below) a sample size of 64 individuals per site would be required. For objective 3 (see below), power analysis indicated a sample size of $n = 33$ (16.5 per area) would be required. All sample sizes were based on an estimated medium effect size with an alpha value of 0.05 (Cohen 1992).

After preliminary visits, the only species that fit both requirements was the chiffchaff (*Phylloscopus collybita*). The species was present in high numbers at both sites and previous work has shown Chiffchaffs immediately adjust the frequency of their songs when exposed to road noise (Verzijden et al. 2010).

For objective 4 (see below) a large, established population of nest box breeding birds was required. A nest box population of Blue tits (*Cyanistes caeruleus*) at Lancaster University was used to study the effect of aircraft noise on nestlings. Previous work on the endocrine response in adult blue tits has been conducted and baseline corticosterone levels are established (Lobato et al. 2008; Müller et al. 2006).

1.9 PhD aim and objectives

Academic aim

To assess the impact of aircraft noise on vocal communication and ecology of passerine bird species around Manchester airport.

Objective 1- Does aircraft noise influence species composition

To address if aircraft noise influences species diversity and abundance, point counts were conducted throughout the breeding season to quantify the density and abundance of woodland bird species. Point count locations were positioned around the airport and varied in noise exposure.

Objective 2-Does airport noise influence bird song structure

To investigate if aircraft noise influences song characteristics, the songs of chiffchaffs holding territories around the airport were compared to those recorded in a quiet site.

Objective 3- Does airport noise affect signal perception

To address if modifications to territorial song influence male-male interactions playback experiments were used test the signal value of song recorded in noisy areas with those from control areas (Ripmeester et al. 2010).

Objective 4- Does aircraft noise cause stress

To address if noise generated by aircraft is an environmental stressor, corticosterone levels were compared in 11-day-old blue tit chicks between nests exposed to different types of anthropogenic noise. First to identify if aircraft noise is perceived as an environmental stressor and secondly to identify if exposure to intermittent aircraft noise is perceived as more stressful than constant road noise.

Chapter 2: No effect of aircraft noise on bird species distribution and density at Manchester Airport

Abstract – Anthropogenic noise affects the behaviour and ecology of birds and has negative effects on health, communication and reproduction. Noise also modifies community compositions and contributes to reductions in species diversity. Assessments of bird communities in noisy areas have typically focused on continuous noise sources such as roads or urban centres. However, intermittent noise has a stronger effect on birds than constant noise. Here the effects of acute, intermittent aircraft noise are investigated on the diversity of birds in mature woodland close to a major international airport. Using encounter data from point counts, variation in species richness with noise levels are explored. The effect of noise on the number of individuals in areas with noise levels ranging from 50 dB(A) to over 90dB (A) is investigated for the 5 most abundant bird species. The results show that beta bird diversity is not affected by aircraft noise with similar species present in high, intermediate and low amplitude sites. Secondly, results show that for the most abundant species the number of birds occupying woodland habitat appears unaffected by increasing noise levels, however the effects of noise on physiology and overall fitness cannot be excluded. Overall, despite the extreme noise amplitudes generated by aircrafts there is no evidence for an impact on woodland bird diversity.

2.1 Introduction

Anthropogenic noise is one of the main contributors to environmental pollution around urban areas (WHO 1999) and, in contrast to other environmental pollutants, global noise levels continue to rise (Mohammadi 2009). Anthropogenic noise has negative impacts on health, cognition, concentration and sleep in humans (Stansfeld 2003). For wildlife, noise affects breeding success, nest density, predator-prey relationships and species community compositions (reviewed in Slabbekoorn & Halfwerk, 2009).

Noise also disrupts communication and animals that rely on acoustic signalling, such as birds, can be particularly sensitive to increases in environmental noise (Slabbekoorn & Ripmeester 2008). Separating the effects of anthropogenic noise from other confounding anthropogenic influences, such as visual disturbance or habitat alteration, can be problematic. Impacts on bird communities and behaviour have been shown for many other anthropogenic factors. For instance, light pollution has negative effects on reproductive success and changes singing behaviour in European robins (*Erithacus rubecula*) (Kempenaers et al. 2010).

How noise Effects species distributions

There is growing evidence that noise itself plays some part in the reduction of avian biodiversity with negative effects on total number of birds and reductions in species diversity (McClure et al. 2013). This can lead to homogenization of bird communities over large areas through the loss of some species and an increase in the same common species (Slabbekoorn & Ripmeester 2008; Slabbekoorn 2013). Species that are sensitive to noise disturbance generally leave a noisy area only returning when noise levels have returned to normal (Bayne et al. 2008). Certain species are less sensitive to acoustic disturbance than others, even if they are closely related (Conomy, Dubovsky, Collazo, & Fleming, 1998).

One of the reasons for loss of bird diversity as a consequence of noise is signal masking (Brumm & Slabbekoorn 2005; Patricelli & Blickley, 2006). Anthropogenic noise can mask signals required for mate attraction, territory defence and predator avoidance (Grade & Sieving 2016). Birds with low-frequency songs are affected more than those with high-frequency songs, presumably because their songs overlap more with that of the noise. As a result, song frequency is a reliable predictor of species absence and birds that use low frequencies are less abundant in noisy areas (Proppe et al. 2013; but see Moiron et al. 2015).

There is also increasing evidence of non-masking influences of noise on bird communities that can affect both survival and reproduction. Noise affects foraging efficiency with both reductions in time spent feeding and avoidance of hunting in noisy areas (Klett-Mingo et al. 2016; Bautista et al. 2016; Quinn et al. 2006). Whilst data is limited for birds, increases in food handling errors have been reported in sticklebacks (*Gasterosteus aculeatus*) exposed to low-frequency noise (Purser & Radford 2011).

Reduction in feeding activities and reduced foraging efficiency are presumably a result of the distraction effects of noise (Chan & Giraldo-Perez 2010). Noise can distract by monopolising the brains attention to one stimulus over any other (Benoni & Tsal 2013). In addition to affecting feeding strategies, distraction by noise increases predation risk by reducing response latency to a visual threat (Chan et al. 2010). Conversely, living in noisy areas can also result in a decrease in predation risk. Francis et al. (2012) showed a reduction in nest predation when nesting in noisy areas. A possible explanation for these findings is that predators that rely on sound to locate nests avoid noisy areas.

For those born in noisy areas there may be significant fitness costs. Excessive noise exposure during ontogeny can lead to increased deformity rates in bivalves (de Soto et al. 2013). Eggs laid in nests that experience high levels of anthropogenic noise have higher mortality rates and slower

growth rates (Potvin & MacDougall-Shackleton 2015). Fledgling success rates are also reduced in nests affected by high noise levels (Halfwerk, Holleman, et al. 2011).

How noise affects species compositions

In addition to affecting the number of species, noise can also influence the composition of avian communities. Noisy territories, or the males that occupy them, may be perceived as lower quality by potential mates. Ovenbird (*Seiurus aurocapilla*) territories in noisy areas are 17% less likely to attract mates than those with territories in quiet areas (Habib et al. 2006). In areas experimentally exposed to road noise the age structure of migratory birds is altered with fewer older birds (Mcclure et al. 2016) or more younger birds holding territories (Habib et al. 2006). These changes to population demographics may have long-term consequences as younger birds tend to be less efficient foragers (Heise & Moore 2003), are less likely to attract a mate (Habib et al. 2006) and have lower reproductive output (Holmes et al. 1996).

Much of the previous work on noise has focused on road noise and that generated from industrial drilling, and there is currently no information on how species compositions respond to noise generated by airports. Airports do affect the singing behaviour of birds by either causing a shift in the timing of songs to reduce any overlap (Gil et al. 2014; Dominoni et al. 2016) or by modifying frequency parameters (See chapter 3 of this thesis). The limited data that are available on other behavioural responses focus on within species comparisons or descriptions of individuals living in areas around military airports where flight movements are relatively few (Ellis et al. 1991). Results show that whilst high amplitude aircraft noise does affect startle responses in the short term, overall the impact is generally low as birds quickly habituate to the disturbance.

The objective of this study was to assess the impact of commercial aircraft noise on the abundance and diversity of woodland bird species close to

Manchester airport. Commercial aircraft noise shares the amplitude levels associated with military aircrafts; however, the number of movements per day is higher. Species richness was compared between locations exposed to varying intensities of aircraft noise to assess the impact of aircraft noise on species diversity. Secondly, to assess the impact of noise on the species communities, species dissimilarity was compared between sites. Species dissimilarity compares the type of species that make up the assemblages of communities between discrete areas. Finally, to investigate the impact of aircraft noise on species abundance, the effect of noise level on the number of individuals for the 5 most common species was explored.

2.2 Methods

Study site

To assess species distribution and breeding bird density, point count surveys were conducted in woodland areas around Manchester airport. Manchester airport is the third busiest in the UK with on average 450 flight movements per day (CAA 2015). Whilst low aircraft activity occurs overnight, aircraft movement levels are consistent throughout the day. There is however a peak in movements during the hours of 0600 and 1000 (Fig. 2.1a). During peak times, a flight movement occurs every 90 seconds, however even during the middle of the day there is a flight movement on average every 2 minutes.

Since the opening of runway 2 in 1997, Manchester airport group (MAG) have managed 350 hectares of land surrounding the site as part of its environmental mitigation responsibilities. This area is predominantly arable farmland with areas of woodland, scrubland and wildflower meadows. For this study five areas of woodland within a 4km distance were identified by using land cover and satellite image data in QGIS (QGIS development team 2014) (Fig. 2.1b).

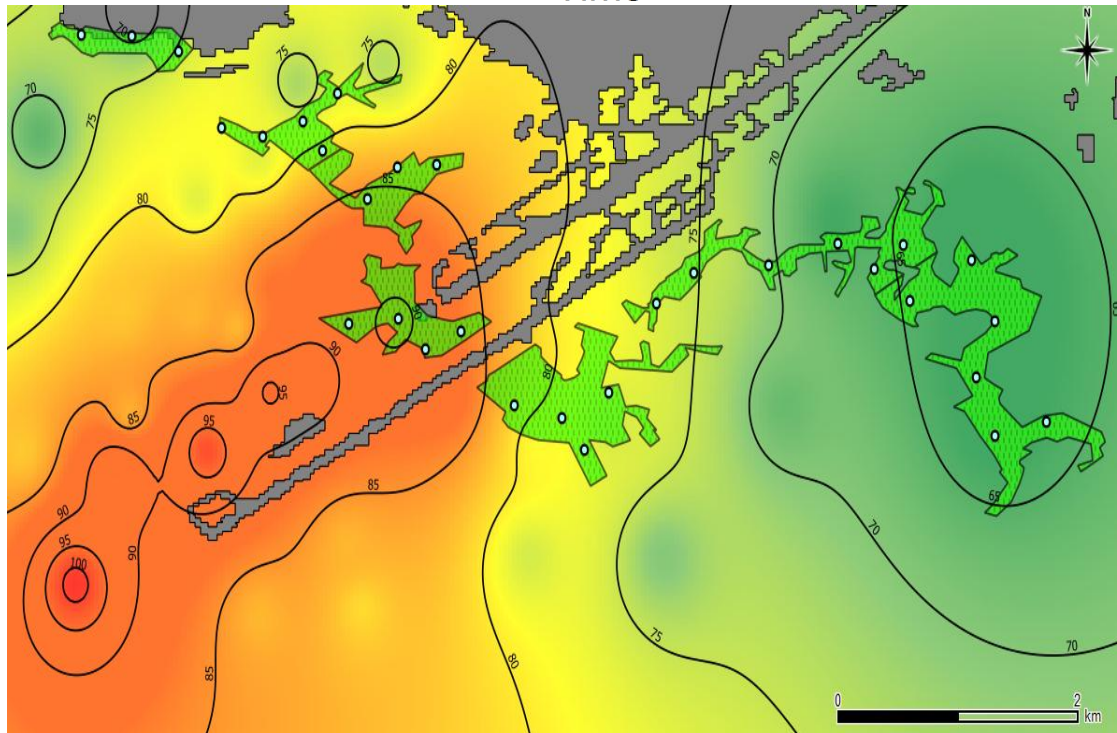
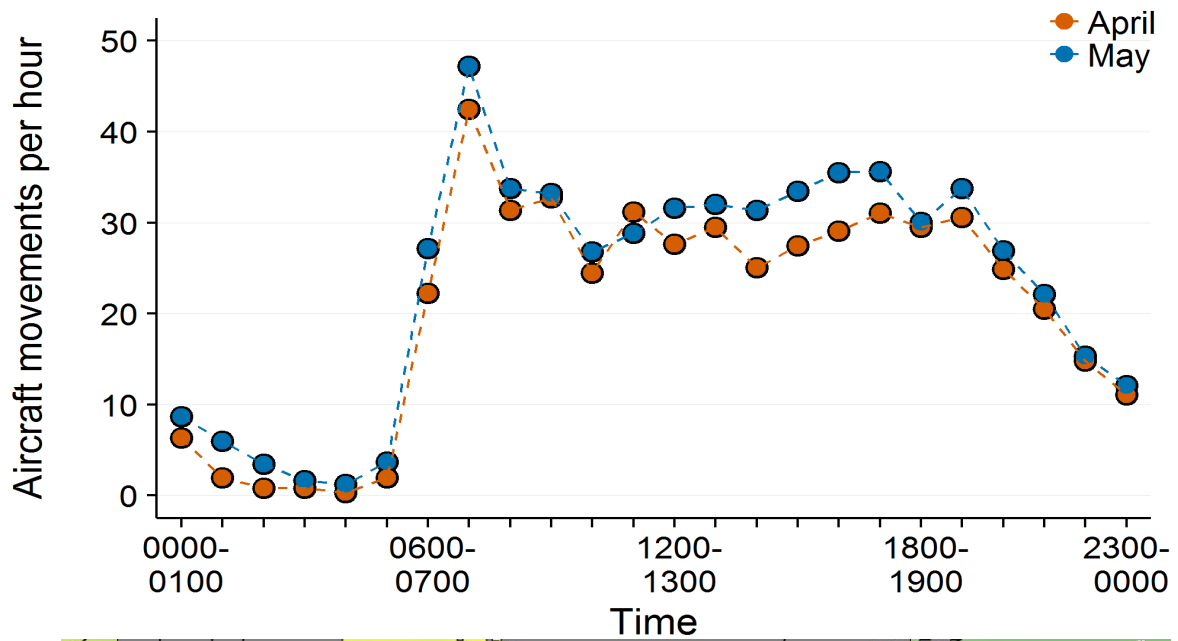


Figure 2.1: (A) Average number of aircraft movements per time bin per day in April (red line) and May 2016 (blue line) from Manchester airport. (B) Heatmap of noise levels in the study area for assessing distribution and abundance of bird species around Manchester international airport. Heat map displaying the noise levels typical of the study site between the hours of 0600-1200. Noise levels were obtained during four independent 10 minute periods between April 1st 2014 and June 30th 2014. Noise levels were logged every second using a Cassella CEL-246 sound level meter. Green polygons indicate woodland areas where point counts took place. White dots indicate point count sites. Values on isobars indicate maximum noise exposure (dB(A)) recorded at each point count site.

Polygons of the five study areas were made in QGIS for each woodland area. The woodland areas were ground-truthed by exporting the coordinates of the perimeter of the polygons and visiting them before point counts took place. Where the woodland edge did not match the polygons generated in QGIS, polygons were edited with data collected during the truthing. The total area of woodland surveyed covers approximately 470 hectares. Thirty-five point count sites were randomly generated using the random point generator in QGIS. This was the maximum number of point count locations that could be generated without violating the assumptions of being within 200meters of a neighbouring point count site (Marsden 1999) or within 50 meters from the woodland edge. Each site was visited prior to conducting the point counts to ensure it was within woodland.

All point counts were conducted between 0500 and 1000 between 1st May and 30th June 2014. Surveys were conducted during the peak breeding season as it was assumed that territories would be established and populations would be more stable with little migration. Point count sites were reached using a hand-held GPS (Garmin E60, www.garmin.com). Upon arrival at the point count, a two-minute rest period was observed to reduce the impact of observer presence. Each point count consisted of a five-minute observation period during which bird species and the number of individuals for each were recorded by both visual and audible detection by a single observer (AW). Distance to each bird detected was measured using a laser range finder (Bushnell) from a fixed point at the centre of the point count site. Additional data collected was the sex of the individual (where possible) and if the individual was heard singing. Birds observed in flight were not included. To ensure an accurate representation of the species present at each point count site, each site was visited four times over the study period.

To reduce potential biases of seasonality and time of day, the date and time that each point count was conducted was randomly generated. Times were generated using the random number generator function sample in R (R Development Core Team 2013). As noise exceeding 45dB(A) has been found to impair detection (Ortega & Francis 2012), point counts were only conducted in quiet periods between aircraft noise events (take-off or landing). Point counts were not conducted in heavy rain or if wind speed exceeded 2 on the Beaufort scale (Bibby et al. 1992). Before any data were collected, AW performed bird identification competency tests using the species identification tool, Bird ID (www.birdid.no). Tests were conducted weekly throughout the study period and a score of >90% of species correctly identified was achieved.

Habitat

To control for variations in species richness due to habitat differences, habitat was assessed for all point count sites. Four measures were used to assess vegetation. (1) Tree height, determined by measuring the height (m) of all trees within a 50 metres radius from the centre of the point count site. (2) Canopy cover, the percentage of sky obscured by plant growth directly above the observer (AW). Canopy cover was estimated at 10 m intervals from the centre of the point count and averaged to give a single estimate per point count. (3) Tree density, derived by dividing the total number of trees within 50 metres of the point count by the total area of the point count site. (4) Tree species, the number of tree species within 50 metres of the point count.

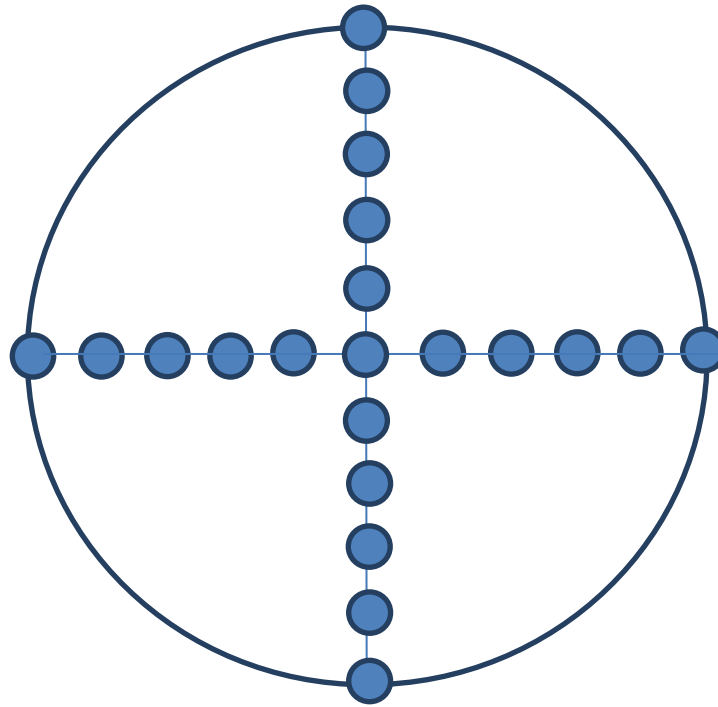


Figure 3: Schematic of sampling area for collection of habitat data from point count sites around Manchester airport. Blue dots indicate points 10m apart used for assessing canopy cover

Sound measurements

Sound measurements were taken over a ten-minute period immediately following each point count with a Casella 346 sound level meter (<http://www.casellameasurement.com/>). The sound level meter was vertically mounted on a tripod set 2m from the ground at the centre of the point count site. A-weighted, fast-response amplitude measures were logged once per second and averaged to generate average amplitude. Average and maximum amplitudes were recorded at each of the point count visits and means were calculated to provide a single value for average and maximum amplitude.

Statistical analysis

To assess the impact of noise on avian communities, species richness (beta diversity) was compared for each point count. Species richness per site was calculated by summing the cumulative number of species detected at each point count site. Values used for assessing species abundance were the maximum number of detections for each species, from any of the four point count visits. Using the maximum number of birds can be seen as the absolute total for each species at a point count site (Forrest & St. Clair 2006). Comparisons of absolute beta diversity values do not account for changes in species composition. To explore changes in species composition between point count sites a Bray-Curtis dissimilarity index was used. The Bray-Curtis index compares species composition between sampling locations and allows for any species replacements. To assess the impact of noise amplitude on dissimilarity each point count site was allocated into one of three amplitude bands based on the maximum amplitude levels recorded. The three bands were (1) sites with maximum noise levels between 50 and 60 dB(A) SPL, (2) between 60 and 70 dB(A) SPL and (3) sites with noise levels exceeding 70 dB(A). to compare the differences in dissimilarity between noise bands Adonis models were built (using Adonis2' function in the 'Vegan package') to compare beta diversity between amplitude bands. Maximum amplitude and distance were added as additional covariates. Adonis models allow the comparison of grouped distance data that violate assumptions of normality and are analogous to non-parametric MANOVA tests (Anderson 2001).

To identify if any of the species were indicative of quiet or noisy sites, species Indicator analysis was applied using the 'Indval' function from the 'labdsv' package (Roberts 2007). Indval generates an indicator value of a species based on relative abundance and relative frequency of each species for each point count (Duffrene & Legendre 1997).

To assess species density, the use of distance sampling was intended to be used; however, none of the species met the minimum number of 60 detections recommended for distance analysis (Sutherland 2006). As sample sizes below this number are likely to give unreliable results, distance sampling was only conducted for the two most common species (Wren $n = 51$ and robin $n = 47$). Species detection distances were binned into 10m intervals and truncated to 50m. Half normal, Hazard-rate and uniform key detection functions were fitted. The best model with the most appropriate key detection function was selected using the lowest AIC. Due to habitat homogeneity, habitat variables were not added as covariates as there would be no effect of varying habitat on detection probabilities. To estimate density per amplitude category (quiet = 50-60 dB(A), intermediate (60-70 dB(A)) and noisy (>70 dB(A)), amplitude band was included as a stratification layer. Secondly, generalised linear models assuming a Poisson distribution were built for the 5 most common species detected during the point counts (Table 1). Generalized linear models are suitable for modelling count data as they are robust to violations of assumptions of normality often encountered with counts (O'hara & Kotze 2010). The number of detections at each point count site was analysed as a function of maximum noise amplitude. To control for anthropogenic disturbance not related to noise and any changes in species occurrence due to seasonal variation, distance to runway and Julian date were included as covariates. Following exploratory data analysis, habitat variables were not included in further analyses as there was no significant variation between any of the four variables between point count sites (Appendix 1). Model selection was based on Akaike information criteria (AIC) scores (Zuur et al. 2009). All data analyses were performed in statistical software package R (R core team 2016).

2.3 Results

Habitat

There were no significant differences detected between any of the habitat variable between point count locations (Appendix1).

Noise levels

Maximum noise levels generated by aircraft for each of the point counts varied between 61.6 and 91.0 dB(A) SPL (Table 1). Average amplitudes for each of the locations varied between 52.3 and 60.9 dB(A). Maximum and average amplitude were highly correlated ($r>0.80$) between point count sites so average amplitude was removed from any further analysis.

Species diversity

A total of 391 birds and 25 species were detected during the point counts (Table 1). Of these 25 species, only nine were detected twenty times or more. Species richness for woodland areas ranged from 18 to 21 with the lowest number of species observed in the noisiest woodland (Table 2.1). Wren (*Troglodytes troglodytes*), robin (*Erithacus rubecula*) and blackbird (*Turdus merula*) were the top three species in each of the three amplitude bands (Appendix 2), six of the 25 species were never detected in the loudest locations and three species were not detected in the quietest locations. Overall the point count site with the highest species richness was in the 60-70 dB(A) (17 species) band and the lowest in the >70dB(A) band (13 species).

Table 2.1: Summary of maximum amplitudes, average amplitudes and species richness recorded in 5 woodland areas around Manchester airport.

Site	Point count (n)	Max amplitude	Average amplitude	Species richness
Rossmill wood	8	61.6	52.3	21
Sunbank wood	8	66.6	55.2	21
Runway 1 wood	5	91.6	60.9	18
Runway 2 wood	6	89	58	20
Quarry bank mill	8	65.6	53.2	20

Community dissimilarity

Adonis models used to compare beta diversity between amplitude categories detected no differences in dissimilarity as a function of maximum amplitude ($F = 1.08$, $P = 0.38$; Fig.2.4), distance from runway ($F = 1.02$, $P = 0.41$) or the noise amplitude category ($F = 1.96$, $P = 0.28$; Fig. 5).

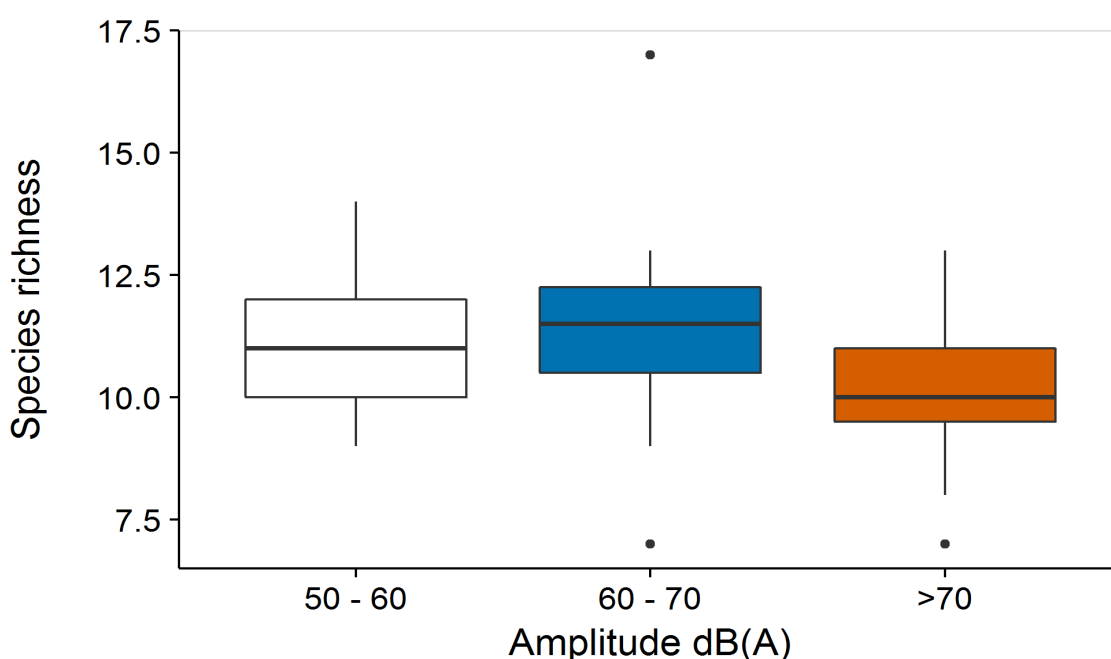


Fig 2.4: Summary of woodland bird species diversity in three noise bands around Manchester international airport. Noise bands were characterised by the maximum amplitude measured during aircraft moments at point count sites in mature woodland. Species richness was derived from observations of bird species during 5-minute point counts conducted throughout the 2014 breeding season.

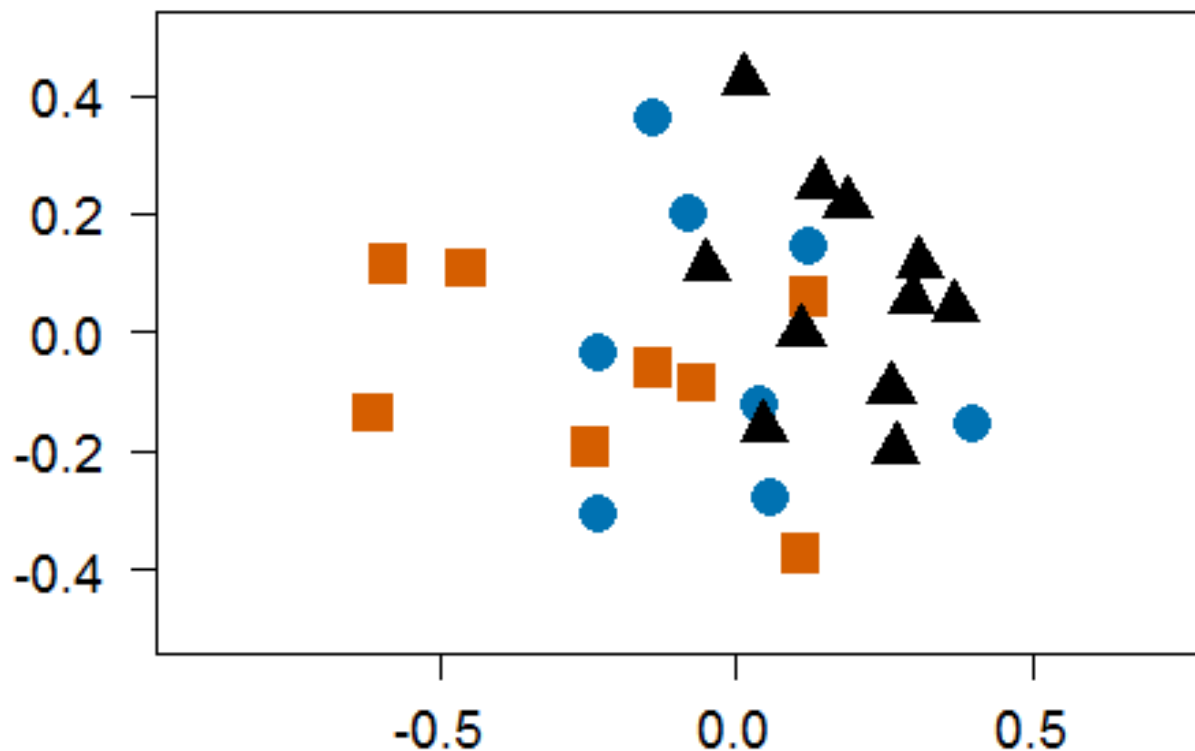


Figure 2.5: Dissimilarity of bird communities from sites around Manchester airport. Dissimilarities calculated using Bray-Curtis dissimilarity index. Each point represents a study site; sites that are more similar are closer to each other on this plot. Red squares indicate site with amplitude levels > 70dB(A), blue circles indicate amplitude levels between 60-70dB(A) and black triangles indicate sites exposed to amplitude levels between 50-60dB(A)

Indicator species

Results from the indicator species analysis identified one species, the Long tailed tit (*Aegithalos caudatus*), as significantly associated ($p = 0.02$) with noisy sites having higher relative abundances and occurrences in sites with higher maximum amplitudes (>70dB(A)). Goldcrests (*Regulus regulus*) were identified as significant indicators of quiet sites ($p = 0.003$) having higher relative abundances and higher occurrences in quiet sites (50 -60 dB(A)). The indval analysis did not identify any indicator species for the 60dB(A) noise band

Distance sampling

For wrens models with half-normal detection function with two cosine adjustments had the lowest AIC. However, as the model with the hazard rate key detection function was within 2 AIC points both were tested for goodness of fit using visual inspection of QQ plots and Shapiro-wilks test for normality. After visual inspection of plots and normality testing (Appendix 3a), the half normal was selected for estimating wren abundance and density estimates. For robins models with a hazard-rate detection function with no adjustments had the lowest AIC. The model with Hazard-rate key detection function and two polynomial adjustments was within 2 AIC points however no improvement to the detection function was observed (Appendix 3b). Density estimates for wrens show lower estimates of abundance and density in the 50-60 (quiet) band, compared to the 60-70 (intermediate noise) band and >70 (noisy) bands. Estimates of abundance and density for robins are higher in quieter sites (table 2.2, figure 2.6).

Table 2.2: Summary of density and abundance estimates for wrens (*Troglodytes troglodytes*) and robins (*Erithacus rubecula*) around Manchester international airport. For both species, estimates from the model with the lowest AIC are reported (Appendix 3A&B).

Species	Amplitude band	Abundance	SE	Density	SE	CV
Wren	50-60	1082.519	21.432	612.100	159.127	0.259
	60-70	1564.341	311.810	894.537	178.310	0.199
	>70	1017.803	300.205	847.490	249.971	0.295
	Total	3664.662	762.328	776.698	161.574	0.208
Robin	50-60	1393.029	251.521	103.322	24.784	0.254
	60-70	1939.49	441.410	137.2	29.118	0.228
	>70	990.862	359.980	99.644	24.412	0.258
	Total	4323.381	1052.911	340.166	78.314	0.74

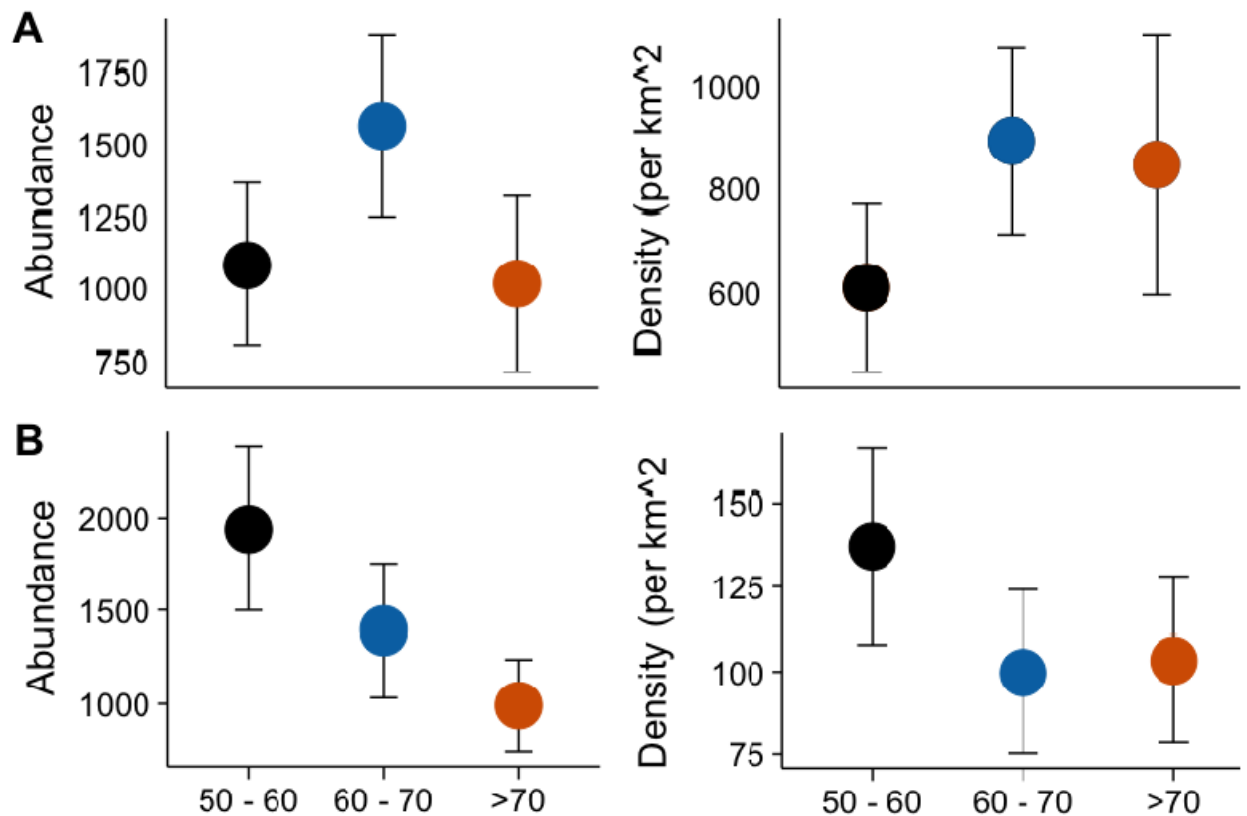


Figure 2.5 Species abundance and density estimates for (A) wrens (*Troglodytes troglodytes*) and (B) robins (*Erithacus rubecula*). Values derived from point counts conducted around Manchester airport. Amplitude bands indicate the maximum amplitude level that was recorded during an aircraft movement event. All point counts were conducted in periods of quiet between noise events.

Number of individuals

For all species comparisons, the model that fit the data best contained only the variable 'Maximum amplitude'. However, there were no significant effects (all values $P > 0.05$) of maximum amplitude on the number of individuals detected for any of the top 5 species (Fig.2.7)

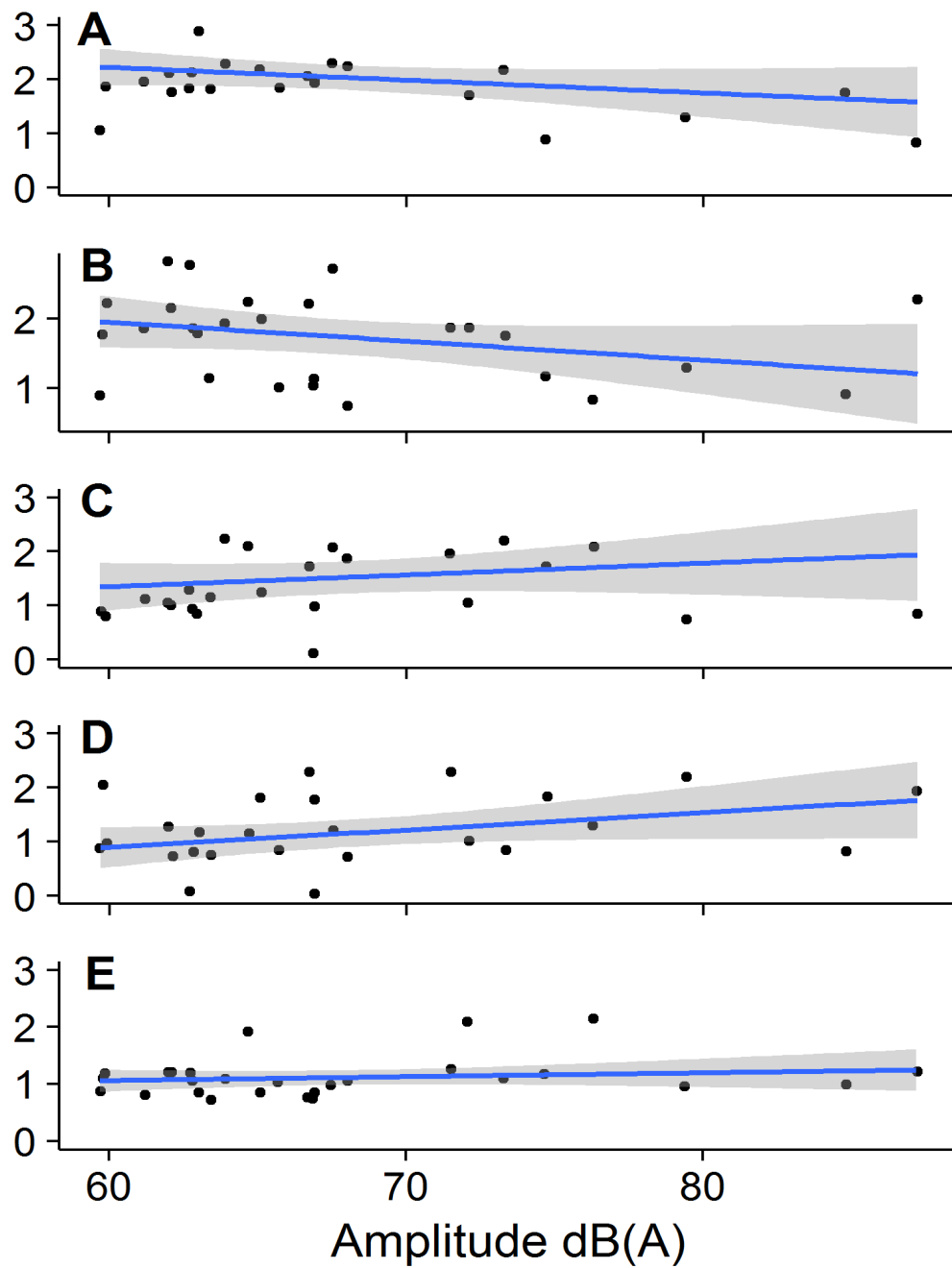


Fig 2.7: Total number of the five most common bird species detected during point counts in woodland around Manchester airport. (A) Wren (*Troglodytes troglodytes*), (B) Robin (*Erithacus rubecula*), (C) blackbird (*Turdus merula*), (D) blackcap (*Sylvia atricapilla*), (E) blue tit (*Cyanistes caeruleus*). No significant effect of amplitude was detected on the number of any species present at any point count site (all $P > 0.05$)

2.4 Discussion

This study addressed the impact of aircraft noise on avian communities by comparing community dissimilarity, species diversity and species abundance among sites that varied in average and maximum noise levels caused by aircraft movements. Firstly, results show that species composition (beta diversity) did not differ significantly between areas affected by aircraft noise. However, some species were not detected in noisier locations, even when habitat and proximity to runways are accounted for. However, the species that were not detected in noisier sites were those with low numbers of detections throughout the whole study area. The absence from noisy sites may simply be through an overall low abundance of these species in the area rather than as a result of noise exposure. There was however no significant dissimilarity between beta diversity when sites were pooled together into noise bands. Secondly, results show that species diversity was unaffected by aircraft noise with no difference in the total number of species between noise categories. Finally, Species density and abundance estimates for the two most common species show conflicting patterns. For the most commonly detected species, wrens, density and abundance was estimated to be higher in the intermediate and noisy sites. Estimates for robins however are for a higher abundance and density in quieter sites and the abundance of the five most common bird species was not affected by increasing noise exposure.

Noise dependent community shift

Here the effects of acute noise from aircraft movements show that there are no differences in either alpha or beta diversity of woodland birds between noisy, intermediate or quiet sites around Manchester airport. These results conflict with previous findings of changes in community composition in response to high levels of noise (Francis et al. 2009).

Results from the indicator species analysis however show that one species, the long-tailed tit, is typical of noisy sites whilst goldcrests were found more frequently and in greater numbers in quieter areas. Avian communities alter in response to noise and one explanation for declines in bird species is signal masking. The effect of noise on birds is frequency dependent (Rheindt 2003). That is birds with higher frequency vocalisations are less susceptible to masking and are able to maintain communication whilst birds with low frequency songs are masked and are excluded from noisy areas (Proppe et al. 2013). Indeed, birds with low frequency songs are less prevalent close to roads with abundance increasing further away (Rheindt 2003). As long-tailed tits use calls that are predominately in the lower end of the frequency spectrum, these results conflict with previous findings suggesting birds with lower frequencies are more likely absent from noisy areas (Hu & Cardoso 2009). Furthermore, goldcrest vocalisations are in the high frequency range yet the species is absent in many of the noisier sites. This suggests that factor(s) other than signal masking are influencing the distribution of these two indicator species. This could be reductions in food, physiological effects (such as stress) or environmental factors not controlled for in this study. It is possible that the same is true for the other woodland species not detected in the sites exposed to high amplitude aircraft noise.

Whilst noise can lead to changes in species compositions and to homogenization of bird communities over a large scale (Slabbekoorn 2013), these changes are not necessarily negative for the individuals. Species that remain in noisier areas can have higher reproductive success (Francis et al. 2009). This can be through reduced competition for territories or the reduction or absence of predators (Francis & Ortega 2012)

Encounters of the five most common species were not affected by noise levels, nor was the overall species diversity affected. Interpretation of these results however require caution, although over 80% of the available habitat was surveyed, the limited number of point counts conducted means the power to detect any differences in species composition is limited. Therefore, the findings reported are likely to be conservative. Additional data including species distributions from other habitat types and from different airports are required to provide more conclusive evidence of community changes or the lack thereof, in response to aircraft noise. Whilst there were no differences in the number of bird species by noise level exposure the presence of a species does not necessarily indicate that they are not affected by the noise (Ware, McClure, Carlisle, & Barber 2015). In ovenbirds (*Seiurus aurocapilla*), a higher proportion of first-year birds occupy noisy territories with older birds occupying quieter sites (Habib et al. 2006). Immature birds have lower reproductive success, presumably because of lack of experience. If changes in age structure as a result of noise exposure are consistent, airports may act as ecological traps where bird populations consist of low quality individuals, unable to establish territories in quieter sites.

In addition to changes in age demographics, migratory birds caught during periods of road noise exposure have lower body condition indexes than those in the same location with no noise (Ware et al. 2015). The reduction in weight of birds may be the result of reduced foraging efficiency caused by increased vigilance (Quinn et al 2006). Aircraft movements also influence feeding behaviour, great tits (*Parus major*) reduce feeding and increase periods of vigilance in response to aircraft noise (Klett-Mingo et al. 2016). If noise generated by aircraft has the same effect on body condition as road noise, the frequent aircraft movements from Manchester airport may contribute to reduced fitness for birds found close to the runways.

Conclusions

The current study contributes to the growing body of work investigating how birds, and other wildlife, are affected by high levels of anthropogenic noise. There were no differences in species compositions in areas affected to high, intermediate or low levels of aircraft noise.

There may however be physiological costs on individuals close to the runways not addressed in this study. Male sage grouse (*Centrocercus urophasianus*) visiting noisy leks have higher corticosterone levels compared to males in quieter areas (Blickley et al. 2012). This effect is greater when the noise is intermittent (Blickley et al. 2012). Higher corticosterone levels in individuals occupying noisy areas may indicate that even if there is suitable habitat, life in noisy areas is more stressful. Elevated corticosterone levels have been detected in humans and rats exposed to aircraft noise (Chen & Chen 1993; Rabat et al. 2006). High levels of corticosterone can have negative effects on the population as increased corticosterone reduces reproductive success and negatively impacts immune responses (Macdougall-Shackleton et al. 2009; Ouyang et al. 2012). Further work into measuring corticosterone in birds exposed to aircraft noise would provide information on how stressful repeated exposure to aircraft noise is.

Chapter 3: Do birds go deaf around airports? Chiffchaffs *Phylloscopus collybita* exposed to aircraft noise sing lower and slower

Abstract- Anthropogenic noise disrupts animal communication and, in extreme cases, results in the displacement of species. Anthropogenic noise typically consists of continuous, low frequency sounds and animals commonly respond by increasing the frequency of their signals, which results in masking release. Signallers also increase signalling rates, presumably to increase the opportunity for detection. Whilst much is known about signallers' response to constant noise, little is known about their response to intermittent, high amplitude noise generated by aircraft movements. Birds living close to airports can be exposed to hundreds of high amplitude noise events (>100dB(A)) every day. These broadband extreme noise levels exceed the releasing capabilities of spectral or temporal modifications and do not provide the signal to noise ratios required for signal detection. Songs of chiffchaffs near two airports in two countries were compared to those found in nearby quieter areas. In contrast to the typical findings, results show that airport birds sing songs with lower frequencies and slower song rates than those in quieter areas. Whilst these results are not consistent with those expected for improving signal detection in noise, they are consistent with the changes in songs of deafened birds. These findings may be the first to show that aircraft noise can result in sound detection threshold shifts in wild bird populations and suggest that they may suffer from noise induced hearing loss (NIHL).

3.1 Introduction

Anthropogenic noise is one of the main contributors to environmental pollution around urban areas (WHO 1999) and is accountable for negative impacts on health, concentration and sleep in humans (Stansfeld 2003). In birds, noise can influence breeding success, predator-prey relationships and can alter species community composition (Slabbekoorn & Halfwerk 2009). In contrast to other environmental pollutants, global noise levels continue to rise (Mohammadi 2009). To date, most studies investigating the impact of anthropogenic noise on wildlife were conducted in areas where industrial or road traffic is the primary source. Both have similar sound profiles that typically consist of relatively constant, low frequency noise. Little is known about the impact on signalling behaviour of intermittent, extreme amplitude noise as generated by aircrafts, trains or heavy industry.

Animals that rely on acoustic communication, such as birds, are particularly sensitive to increases in background noise levels (Slabbekoorn & Ripmeester 2008). During transmission, acoustic signals may be subject to interference by environmental noise (Goodwin & Podos 2013). If environmental noise decreases signal-to-noise ratios it is more difficult for receivers to hear all or part of the signal. Noise masking compromises the information conveyed in a signal, with negative results for territory defence and mate attraction (Klump 1996). In general, two main processes can result in signal masking. A signal is masked if its frequency overlaps with that of the background noise (frequency specific masking) (Bacon & Grantham 1989; Hulse 2002) or if the background noise has a broad spectrum and the level is higher than that of the signal. This results in the noise saturating the auditory filters. This results in complete masking where the detection of any sound is not possible (Moore 2012).

In the case of frequency specific masking, many species alter the spectral frequency of their vocalisations to increase SNR and reduce overlap with

noise frequency bands (Bermúdez-Cuamatzin et al. 2011; Goodwin & Podos 2013). Indeed, great tits (*Parus major*) modify song frequency up or down when exposed to experimental treatment of noise playbacks at particular frequencies (Halfwerk & Slabbekoorn 2009). Under noisy conditions birds also increase the number of times a signal is given (Brumm & Slater 2006) or increase the time spent singing, presumably to improve probability of detection (Díaz et al. 2011). Birds also shift the timing of signalling to periods of relative quiet to avoid masking sounds (Egnor et al. 2007). Amplitude increase in response to noise, known as the Lombard effect (Brumm & Zollinger 2011) is also used to improve signal to noise ratios and has been found in every mammal and bird species tested (Hotchkiss & Parks 2013).

Whilst signal modification increases signal to noise ratios and improves signal detectability, the modifications can affect intraspecific interactions (Ripmeester et al. 2010). Birds typically convey information in spectral and temporal parameters (de Kort & Eldermire 2009; Linhart et al. 2012). These parameters are used by receivers to assess condition, motivation and social rank of the sender (Aunay et al. 2014). Noise thus changes acoustic signals resulting in population differences between noisy and quiet areas (Nemeth & Brumm 2009).

Unlike noise generated by road traffic, areas around airports may be relatively quiet punctuated by high amplitude noise events generated by low altitude aircraft movements on approach, on the ground and on take-off (Fig. 3.1). Noise generated by aircrafts frequently exceeds 100dB(A) for territories within 300metres of runways, with the amplitude of the noise building to a peak before tailing off. Noise generated by aircraft can therefore make typical masking release strategies, such as spectral or amplitude adjustment of signals ineffective.

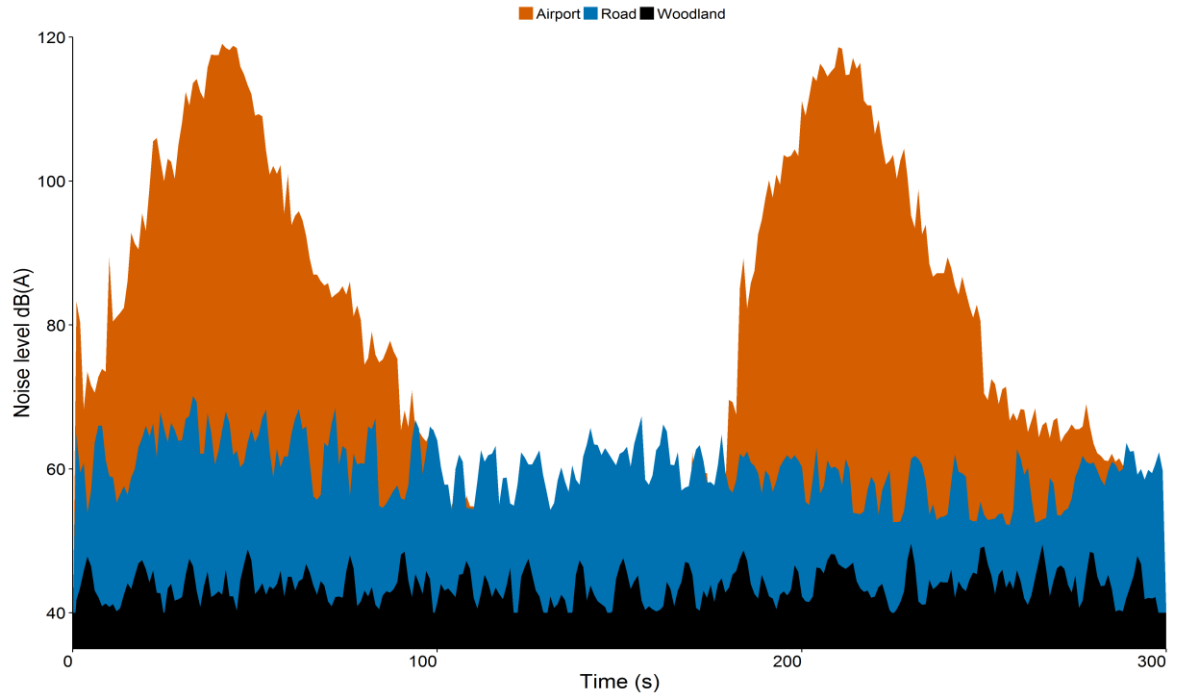


Figure 3.1: Distribution of environmental noise levels dB(A) over a period of 5 minutes in a Chiffchaff (*Phylloscopus collybita*) territory 400 meters from aircraft noise (red area), a chiffchaff territory 150 metres from a road (blue area) and a chiffchaff territory in an isolated woodland (black area). All amplitude measurements were taken every second during the same time of day (0700-0705) using a Casella CEL-246 sound level meter.

This study examines the effects of aircraft noise on the territorial song of the chiffchaff (*Phylloscopus collybita*). Chiffchaffs are a good model species for assessing the impact of anthropogenic noise as they have previously been shown to modify song parameters in response to road noise (Verzijden et al. 2010), probably to increase the distance over which their songs can be heard. Songs recorded around two busy international airports were compared to those recorded in nearby areas with lower noise levels. This is one of the first studies to investigate the effects of aircraft noise on the structure of bird song.

3.2 Methods

Study species and sites

Chiffchaffs (*Phylloscopus collybita*) are summer migrants to Europe, with the first males usually arriving in March. Males defend their territories by singing from strategic positions throughout the breeding season, which typically concludes at the end of June. Chiffchaffs mediate social interactions between males by modifying temporal and spectral song parameters. Fighting ability is signalled with a relatively low peak frequency (Linhart et al. 2012) whilst increasing the duration of songs signals motivation to fight (Linhart et al. 2013).

Song recordings around Manchester airport (450 aircraft movements/day, CAA 2015) and a control site 20km to the southeast were made between 0500 and 1200 from March 17th to June 30th, 2014. Recordings from Schiphol airport (1200 aircraft movements/day, Airport Council International 2015) and a control site 50km south-west, were made in May 2015 in the Netherlands. Data from the Netherlands were obtained through a collaboration with Hans Slabbekoorn at Leiden university. Airport and control sites were visited on alternate days throughout the study period.

Both airports and control sites are characterised by mixed broadleaf woodland and scrubland, with willow (*Salix sp.*), Sycamore (*Acer pseudoplatinus*) and Oak (*Quercus sp.*) being the dominant tree species. A singing bird was observed and all singing posts were marked on a GPS (Garmin 62: www.garmin.com) to build simple territory maps. A territory was classified as a triangulated area from a minimum of three singing posts. A total of 68 territories were identified in the UK and 36 in the Netherlands.

Song recording

To control for confounding effect on song parameters due to seasonal changes, airport and control recording sites were visited on alternate days throughout the study period. Each recording session was preceded by a 5-minute habituation period to reduce the effect of observer presence on singing behaviour. A ten-minute singing session of the target individual was then recorded. Recordings were aborted if the focal male interacted with another individual or if it moved out of sight. To reduce the risk of recording the same individual twice, recordings made within 200 metres of a previous recording were removed from the analysis. This distance exceeds the typical size of chiffchaff territories (Rodrigues 1998). All recordings were made using a Sennheiser ME67 microphone with a Rycote softie windshield, combined with a Marantz PMD661 MKII solid-state recorder (sampling frequency: 44100Hz; 16bit; WAV format). All recordings in the UK were made by AW. Recordings from the Netherlands were obtained from a database provided by HS.

Noise measures

To assess how noise levels impact chiffchaff songs, maximum amplitude for each of the territories in the UK was recorded using a tripod mounted sound level meter (Precision Gold N05CC dB (A), fast response). Average amplitude was obtained by recording the noise levels every second for a 10 minute period (using a Casella CEL-246 noise level meter). Noise data did not violate assumptions of normality so differences in noise levels between the sites were analysed with a two-tailed, independent T-test.

Song analysis

Each individual song from the ten minute singing session was cut from the main recording (mean number of songs per individual = 39.65 ± 6.59). A song was defined as a sequence of syllables where the pause rate between syllables was less than 2 seconds. A song ended when a pause longer than

2 seconds between syllables was detected. For each individual a random sample of ten songs was selected from the database using the sample function, with no replacement, using the statistical software R (R core team, 2016). Measurements from these ten songs were used to generate mean values for each parameter, for each individual. Eight parameters were measured for acoustic analysis (Fig. 3.3) using the automatic parameter measurement feature in Avisoft-SAS Lab Pro version 4.3 (Avisoft bioacoustics, Berlin, Germany). For element separation an automatic single threshold of -21dB was used with a hold time of 100ms.

Spectral parameters measured were the maximum and minimum frequencies within a song (MaxF & MinF), the difference between highest and lowest frequency (BW) and the frequency with the highest amplitude or peak frequency (PF). Temporal parameters measured were the duration of each syllable (SD), duration of the song (DUR), syllable delivery rate

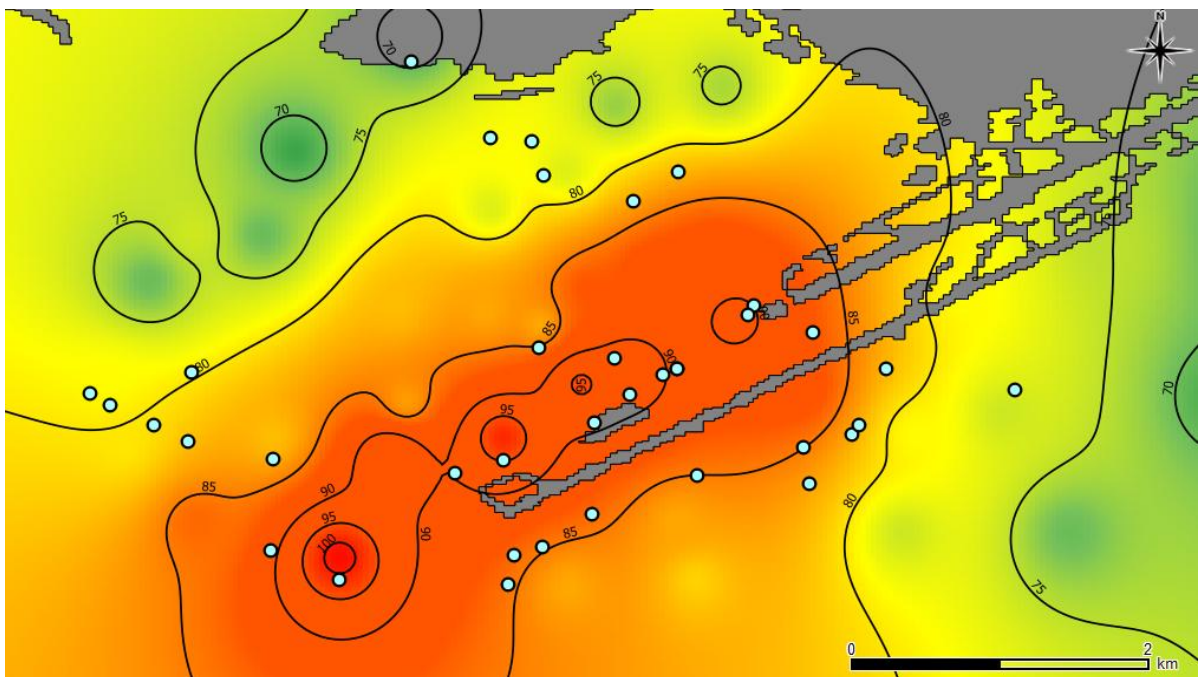


Figure. 3.2: Study Area around Manchester airport testing differences in chiffchaff (*Phylloscopus collybita*) song parameters. Blue dots show location of territories where recordings were obtained. Colours indicate maximum amplitude levels generated from 10-minute measurements of amplitude using a Casella CEL 62 noise level meter.

(SR), and the number of syllables in the song (NS). Syllable delivery rate was derived by dividing the number of syllables within a song by the song duration. For all measurements a Hamming window and an FFT-size of 512 with a 50% overlap was used. Songs were excluded from analysis if the signal-to-noise ratio was too low to allow automatic parameter measurement to identify all syllables in a song. If a song was excluded, a replacement was randomly selected from the database.

Syllable type

The use of syllable types per individual was compared between airport and control sites. Syllable types were first categorised based on the location of the first frequency modulation using spectrograms (Fig. 6). Random samples of 20 from each syllable type were selected using the R sample function with no replacement. Syllables were analysed using the same automatic detection parameters used for song analyses (see above). A discriminant function analysis (DFA) was used to categorise the syllables based on (1) spectral parameters: maximum frequency, low frequency, peak frequency and (2) temporal parameter: syllable length (described above). To objectively categorise the syllables the DFA was first 'trained' with a subset ($n=10$) of each of the syllable types. This trained model was then applied to the remaining syllables in the dataset ($n=10$). The frequency of observed syllable types was then compared to the frequency of predicted syllable types to test the accuracy of the DFA.

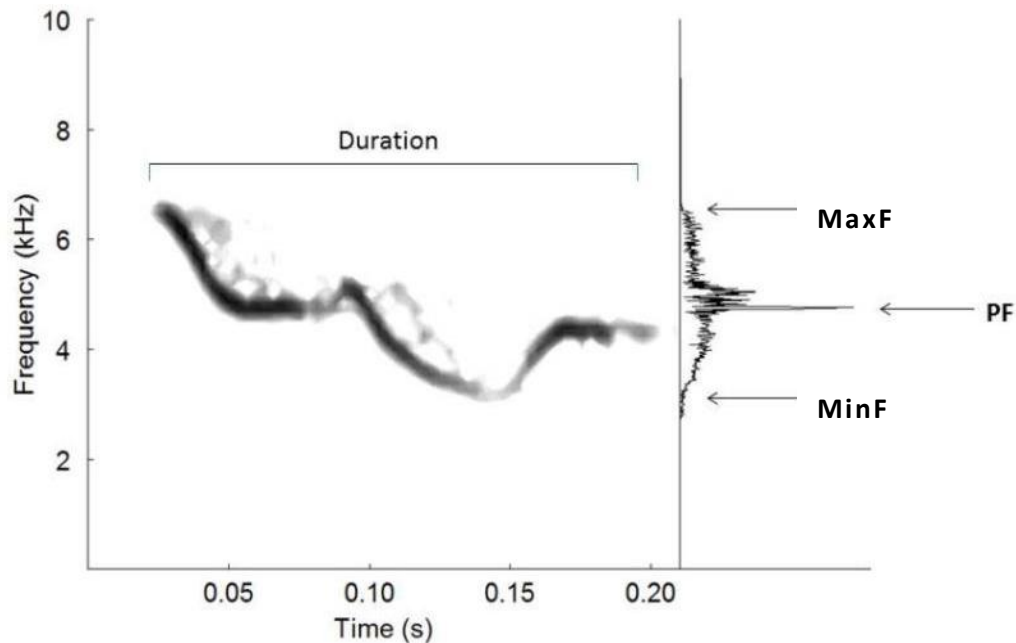


Figure 3.6. Example of chiffchaff (*Phylloscopus collybita*) syllable with measurements used for analysis as indicated. MaxF = maximum frequency, MinF = minimum frequency, PF = peak frequency, Duration = length of syllable in seconds. Spectrogram created in Avisoft (Hamming window, FFT size = 512, overlap of 50%)

Statistical analysis

Thirty eight recordings of individuals from the Manchester airport site and thirty from individuals from the UK control site were used in the analysis. For the Dutch recordings, eighteen airport and eighteen control individuals were used. To ensure independent variables did not violate assumptions of covariance for MANOVA/ANOVA models, pairwise Pearson's correlation tests were performed on both dependent and independent variables prior to model building. The variable 'Number of syllables' was highly correlated with 'Song length' and 'Syllable duration' ($r > 80$) and was removed from further analysis. 'Bandwidth' was highly correlated with 'Peak frequency' and 'Maximum frequency' ($r > 60$) and was also removed from further analysis. The remaining dependent variables were tested for normality and equal variances using Shapiro-Wilks and Bartlett test functions. For UK recordings, no variable violated the assumptions of normality or equal variance between groups. However, only variables minimum frequency, syllable rate and syllable duration showed a normal distribution from the Dutch recordings (Shapiro-Wilks

test for normality all p -values >0.05), therefore for consistency two tailed, non-parametric tests (Wilcoxon signed-ranks) were used throughout.

To test if airport birds sing differently from control birds, song parameters were compared as a function of location (airport or control site) for the UK and the Netherlands. As sample sizes differed between countries, the analyses were conducted separately and effect sizes were used for comparison between countries.

MANOVA models were used to test the impact of noise levels (independent variable) on song parameters (dependent variables) for the UK recordings. Song rates in chiffchaffs vary throughout the breeding season, depending on reproductive status (Rodrigues 1996). To control for this, Julian date of recording was included as a further explanatory term to test for seasonal changes in song parameters. Four models were built for each site, (1) noise amplitude alone, (2) Julian date alone (3) noise amplitude and Julian date and (4) interaction between noise amplitude and Julian date. The model with the lowest Akaike Information Criterion (AIC) value for each site was used for further analyses (Zuur et al. 2009).

Sequential Bonferroni corrections were used to control for multiple testing (Rice 1989), however, given the increased probability of type II errors following correction for multiple testing (Nakagawa 2004) both P values and unstandardized effect sizes are reported. Effect sizes allow comparisons between unbalanced data as they report the size of the difference between two variables (Nakagawa 2004) All data analyses were performed in R (Development et al. 2011) and effect sizes were estimated using the 'effsize' package (Torchiano 2016).

3.3 Results

Maximum and average amplitudes for each territory were highly correlated ($r=0.8$, $p<0.001$) therefore only maximum amplitude was used for the analysis. Comparisons of maximum amplitude between the two UK recording locations showed that noise levels at airport territories were significantly higher than those in control territories (Maximum amplitude airport territories = $81.93\text{dB(A)} \pm 9.11$, maximum amplitude control territories = $57.13 \text{ dB(A)} \pm 4.57$; T-Test- $T= 11.99$, $p<0.001$).

Song analysis

Comparisons of song parameters between airport and control recordings showed airport birds use lower maximum frequencies in both the UK ($N_1= 38$, $N_2 = 30$, $W = 349$, $P = 0.005$, $d = 0.757$) and the Netherlands ($N_1= 18$, $N_2 = 18$, $W = 95$, $P = 0.034$, $d = 0.385$) (Fig. 4). UK Airport birds also use lower peak frequencies ($N_1= 38$, $N_1 = 30$, $W = 279$, $P = <0.001$, $d = -1.099$) and deliver songs at a slower rate ($N_1= 38$, $N_2 = 30$, $W = 374$, $P = 0.015$, $d = 0.660$). No other song variable differed between sites. Overall airport birds sing songs with lower maximum and peak frequencies, delivering syllables at a slower rate.

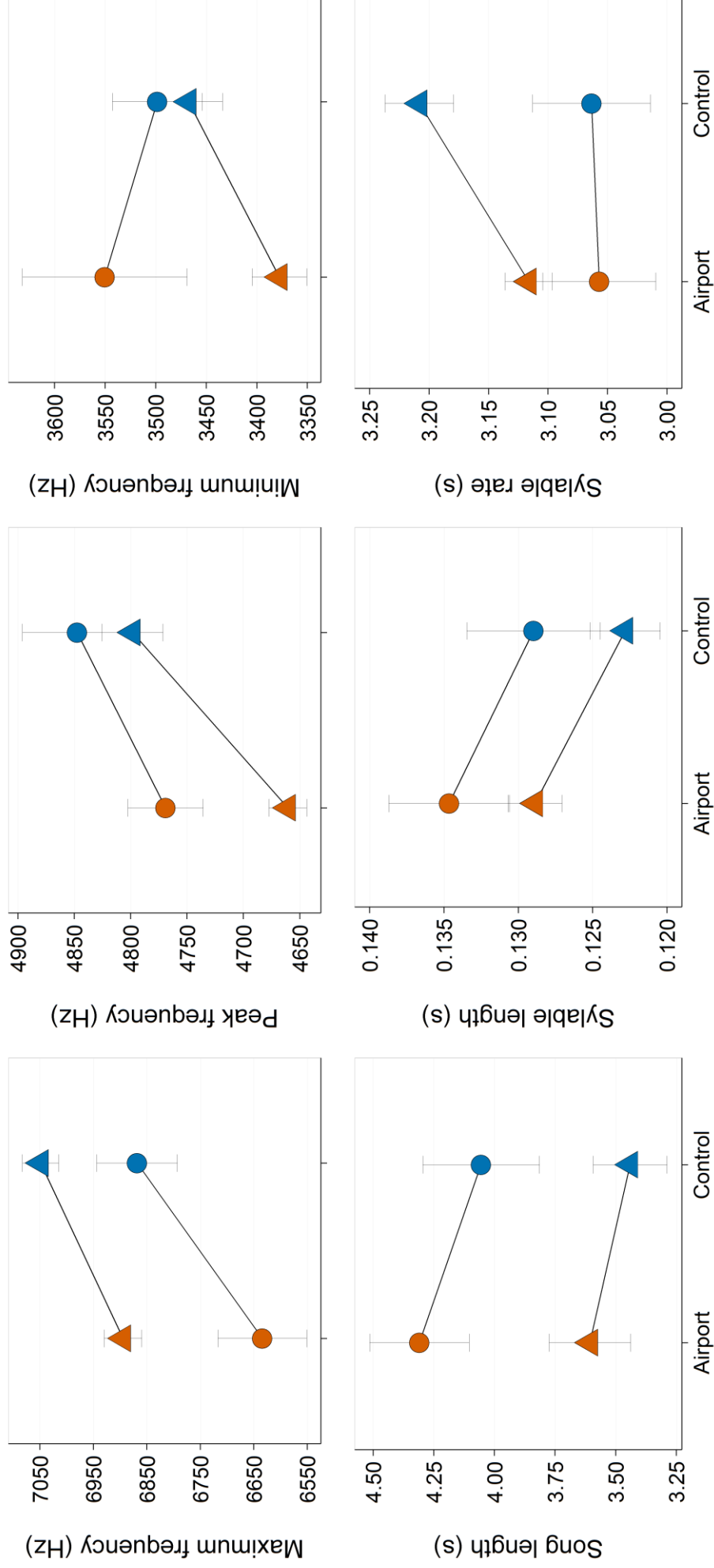
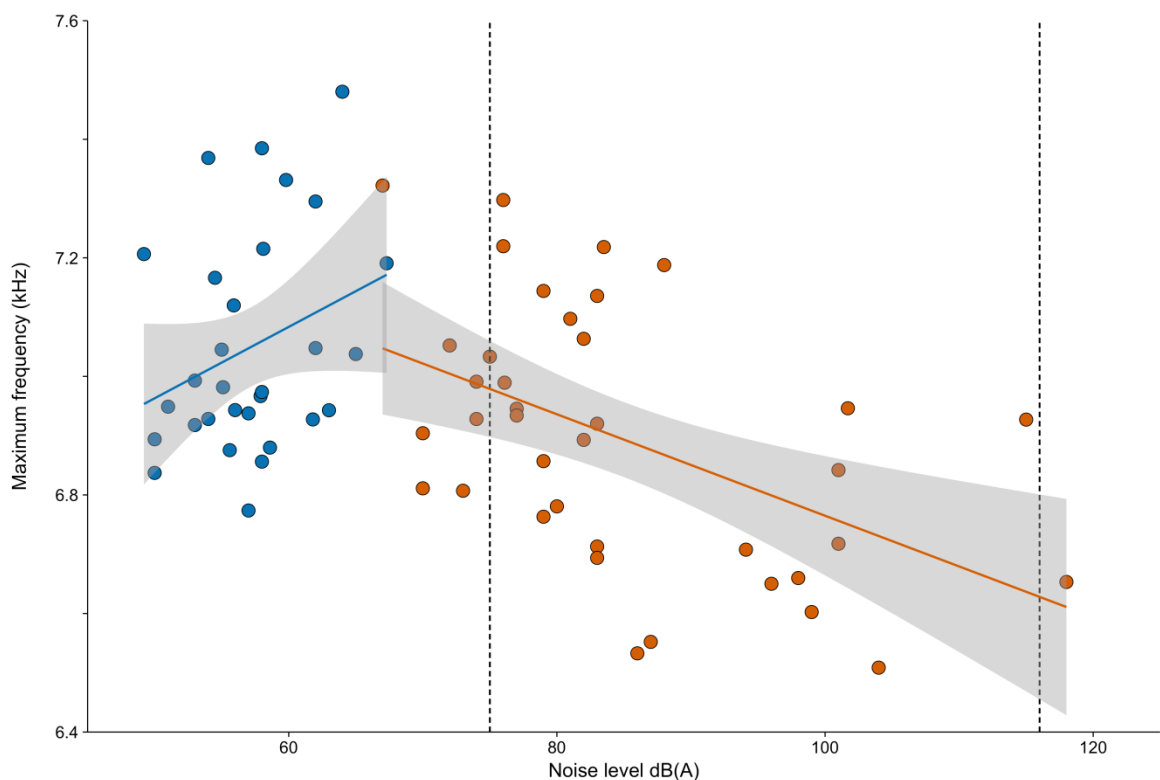


Figure 3.4: Mean values (± SEM) of spectral and temporal variables from chiffchaff (*Phylloscopus collybita*) songs recorded at Airport (red symbols) and control sites (blue symbols). Circles show data for recordings made in the Netherlands (Airport: N₁=18; control: N₂=18), triangles show results of recordings made in the UK (Airport: N₁=38; control: N₂=30). For both the Netherlands and UK populations maximum frequency is significant following Sequential Bonferroni correction. The difference

UK site comparison

The model containing the term 'Amplitude' and 'Julian Date' had the lowest AIC value (table 1). For the airport population, the model showed a significant negative effect of noise level on maximum frequency ($R^2 = 0.28$, $t = -2.054$, $P = 0.001$; Fig. 5) of the song. No effect of noise level was detected in any other song parameter (all variables $P = >0.05$). There was no significant effect of Julian Date on any response variable (all variables $P = >0.05$). For the control site, the model containing the term 'Amplitude' only had the lowest AIC value. The model showed a significant positive effect of amplitude on minimum frequency ($R^2 = 0.11$, $t = -2.17$, $P = 0.039$). There were also significant differences in temporal parameters- syllable length ($R^2 = 0.20$, $t = 2.85$, $P = 0.008$) and syllable rate ($R^2 = 0.22$, $t = -3.00$,



$P = 0.005$). As amplitude increased, control birds sang longer songs at a

Figure 3.5. Maximum frequencies of chiffchaff (*Phylloscopus collybita*) recorded at Manchester airport and a control site. Blue circles represent birds from the control site, red circles represent airport birds. The dotted lines indicate noise levels that result in temporary and permanent threshold shifts (Dooling & A. Popper 2007).

slower rate. There was no effect of amplitude on peak frequency or maximum frequency.

Syllable use

Seven syllable types were identified after visual inspection of spectrograms (Fig. 6). The DFA model discriminated 100% of 5 of the syllable types namely A, B, E, F, and G (see Fig. 6). Discrimination between syllable types C and D was 60% and 40% and therefore they were combined into a single syllable type for further analysis. All syllable types violated the assumption of normality. Therefore, unpaired non-parametric tests were applied to each syllable type. Wilcoxon signed rank tests comparing frequency of syllable use between sites show a significant difference in the use of the syllable types “A” and “G” (WSR test Syllable A: $W=418.5$, $P=0.046$; Syllable G: $W=761$, $P=0.0136$). The control population used syllable type “A” more, while the airport population used syllable type “G” more. No difference in use was detected in any of the remaining syllable types (WSR; Syllable b: $W=550.5$, $P=0.814$; Syllable C: $W=575.5$, $P=0.950$; Syllable E: $W=632$, $P=0.439$; Syllable F: $W=524$, $P=0.523$). There was no effect of seasonality on frequency of usage of any syllable (WSR all: $p>0.05$).

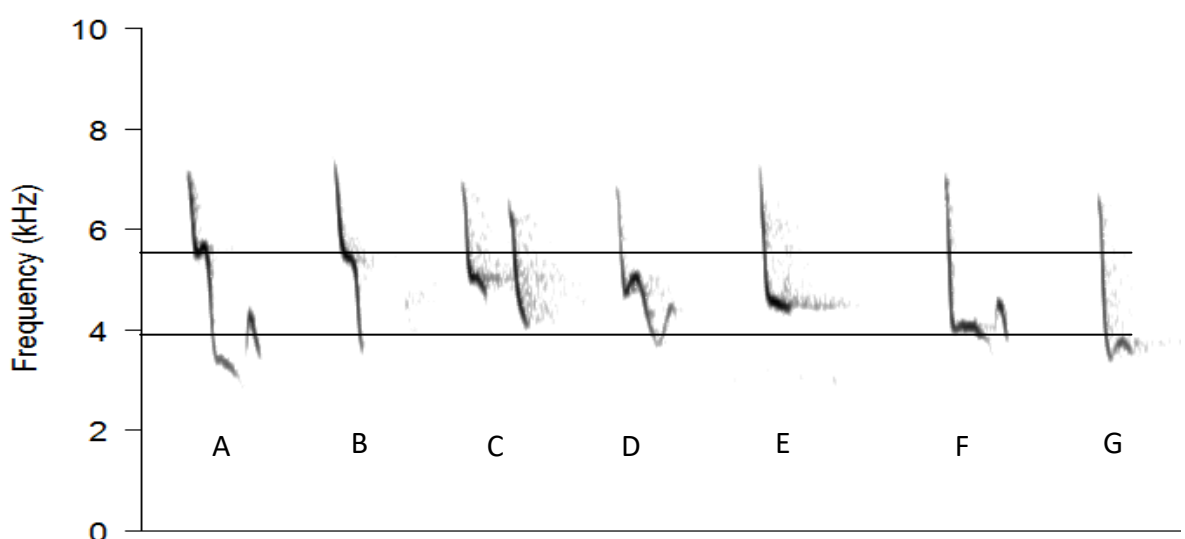


Figure 3.6: Spectrogram of syllable types identified from recordings of chiffchaffs (*Phylloscopus collybita*) in the UK. Syllables are order ranked from highest to lowest peak frequency. Lines indicate frequency shifts used for syllable categorisation Spectrogram created using

There was a significant association of syllable type A ($X^2 = 4.014$, $P = 0.041$) and syllable G ($X^2 = 7.88$, $P = 0.03$) with site. A was associated with the control site and G with the airport site. There were no other significant associations with any other syllable type ($P > 0.05$)

3.4 Discussion

The songs of chiffchaffs exposed to frequent, high amplitude noise events at airports are significantly lower in maximum and peak frequencies and are sung at a slower rate compared to birds from quiet control sites. This result was replicated at two airports in two countries. In addition, the higher the noise levels the lower the max frequency of the songs for airport birds. The clear downward spectral shift is a result of airport birds using more low frequency syllables, rather than an overall drop in frequencies of songs.

These findings contrast sharply with other studies on the impact of anthropogenic noise on birdsong. A common finding is that birds sing at a higher frequency when exposed to anthropogenic noise. This is presumably to improve signal to noise ratios since most anthropogenic noise is low in frequency (Slabbekoorn 2013). These findings show that chiffchaffs exposed to aircraft noise primarily use more syllable types with low frequencies compared to those in quieter areas. Individuals from noisy areas also used fewer syllable types with higher frequencies.

Extending the duration of a signal or repeating the same signal more frequently can also improve signal detection. By offering a better chance of detection during noisy periods (Brumm et al. 2004). Faster delivery rates have been observed in birds living in naturally noisy areas (Brumm & Slater 2006) and following exposure to white noise (Potash 1973). In contrast, as reported here chiffchaffs deliver syllables at slower rates under a regime of aircraft noise, potentially reducing the opportunity for detection.

One explanation for these findings is that they are not strategies to improve signal detection but rather artefacts of noise induced hearing loss. The findings mirror those found in surgically deafened birds that also show both reduced song frequency and song rates (Watanabe & Sakaguchi 2010; Watanabe et al. 2007). In these studies budgerigars (*Melopsittacus undulatus*), Bengalese finches (*Lonchura striata domestica*) and zebra finches (*Taeniopygia guttata*) all showed slower song rates with values similar to those detected here in chiffchaffs. Frequency shifts in the three species ranged from a decrease of around 100-400 Hz, again very similar to the 150 Hz difference found in birds exposed to aircraft noise.

Hearing loss occurs when detection thresholds for a signal are increased due to damage to the inner hair cells. Dooling & Popper (2007) suggested infrequent exposure to bouts of sound >90 dB(A) are sufficient to permanently raise detection thresholds in birds. Aircraft noise at Manchester airport regularly exceeds this level at distances up to 800 meters away (AW pers. Observation). In addition, long term exposure to lower amplitude levels can also result in detection threshold shifts (Dooling & Popper 2007). Noise induced hearing loss has been observed in birds exposed to noise exceeding 95dB(B) for 200 days (Marler & Konishi 1973). Rats exposed to simulated airport noise at amplitudes of 88dB SPL, showed signs of hearing loss after 9 days exposure (Rabat et al. 2005) and fish show threshold shifts following ten minutes of 160-170dB re 1 μ Pa noise exposure (Smith et al. 2004). Repeated exposure to noise, even at lower amplitudes, can prevent the recovery of the auditory system and lead to cumulative noise induced hearing loss (Eggermont 2016). Duration required for cell recovery varies depending on the amplitude of the noise but can be between 1hr and 72hrs (Saunders et al. 1974, Murphy et al. 2011). Birds living close to Manchester airport are exposed to between 20 – 50 aircraft movements per hour (Fig 2.1) and noise generated by aircraft movements typically exceeds 80dB(A) for approximately 30 seconds (Fig

3.1). This results in birds living close to the airport being cumulatively exposed to a sound exposure level (SEL) exceeding 80 dB(A) for 30 minutes every day. This duration of exposure, along with this intensity would be sufficient to at least cause TTS (Eggermont 2016) and may possibly result in PTS.

The number of aircraft movements, the temporal frequency and the amplitude levels generated are sufficient to raise detection threshold for bird species living close to the airport and thus result in at least partial hearing loss.

There are at least three mechanisms by which hearing loss may lead to the spectral and temporal changes of songs. Firstly, birds require auditory feedback of their own song to acquire and maintain their song structure (Watanabe et al. 2007). Following chemical induced hearing loss, decreases in fundamental frequencies and loss of syllable structure occurs in zebra finches (*Taeniopygia guttata*) (Price 1979). However, the partial loss of hearing does not necessarily result in alteration of songs. Loss of hearing between 3-10 kHz does not affect song maintenance of Bengalese finches (*Lonchura striata domestica*) (Woolley & Rubel 1999). The loss of frequencies below 3 kHz does result in loss of high frequencies and reduction in song stability (Woolley & Rubel 1999). As the dominant noise generated by aircraft is below 3 KHz (AW per obs), repeated aircraft noise exposure would result in the loss of frequencies required to maintain auditory feedback. Therefore noise induced hearing loss would result in the loss of auditory feedback and may explain the dominance of low frequency syllables in airport birds.

Second, selection may favour low frequency songs in a population with hearing impairment because these are more likely to be perceived by partially deaf birds. In progressive hearing loss, the ability to detect high frequencies is lost before those of low frequencies (Holme & Steel 2004). Thus, high frequency songs may not only be selected against through a

lack of auditory feedback from their own song but also from a lack of response from the receiver.

Whilst the results are consistent with those found from birds experiencing hearing loss, there are other explanations that cannot be excluded with the current data. A commonly observed response to low frequency anthropogenic noise is the use of high frequency syllables or an upward shift in frequency presumably to reduce the amount of overlap between masking noise and the signal (Slabbekoorn 2013). Indeed, chiffchaffs exposed to road noise show an immediate upward shift in minimum frequencies (Verzijden et al. 2010). However, noise exposure in the current study differs dramatically in amplitude from typical anthropogenic noise in both amplitude and temporal distribution (see introduction). The high amplitude of sound levels across the spectrum from aircraft movements may exceed a threshold where the modifications of spectral characteristics do not aid in masking release. Quadratic relationships, that is an observed change in response to low noise but not to high noise levels, have been observed for both temporal and spectral signalling characteristics in birds exposed to noise levels exceeding 70dB(A) (Díaz et al. 2011; Brumm et al. 2009). Domestic chickens (*Gallus gallus*) and serins (*Serinus serinus*) increase frequencies and song rates, in response to noise up to about 70dB(A). At noise levels higher than 70dB(A) birds revert to using songs comparable to no noise being present. This quadratic relationship may be explained by the birds' reliance on self-auditory feedback and maintain a feedback loop (Brumm et al. 2009). However, it is unlikely that this process can explain the data in the current study, since the Maximum Frequency values are lower under noisy compared to quiet conditions, rather than equal. If noise levels are at amplitudes that compromise the auditory capabilities of an individual, signallers may be required to switch to a non-auditory feedback mechanism. In this instance, lower frequency slower songs would be perceived better than fast, high frequency songs (Watanabe et al. 2007). However, in this study,

songs were only measured during periods between noise events. As chiffchaffs are capable of immediate adaptation of signals, and if there is a quadratic response, lower frequencies would only be used during noise events and not between as reported here. Therefore, it is unlikely that the observed modifications of song parameters are the result of a quadratic response.

Finally, songbirds often show geographic variation in song structure as a result of the cultural transmission of song combined with adaptation to local transmission characteristics. Little information is available regarding philopatry in breeding chiffchaffs although wintering birds show low site fidelity (Catry et al. 2003). Given the relative close distance (<20km) between airport and control sites, and the fact that the results are replicated at two sites in different countries the observed variation is unlikely to be due to isolation by distance or by adaptation to varying habitat types.

Conclusion

Here the first evidence that acute, frequent and unpredictable noise produced by aircrafts leads to song modification in chiffchaffs. These findings contrast sharply with those seen when exposed to low amplitude, consistent noise, such as observed near motorways. The most plausible explanation for this finding is that the intensity and frequency of aircraft noise results in detection threshold shifts and partial deafness in chiffchaffs, and most likely other species, in the area.

Chapter 4: Increased territorial aggression in birds exposed to aircraft noise

Abstract- Chiffchaffs exposed to high amplitude aircraft noise sing songs with lower maximum frequencies and at a slower song rate than birds in nearby quieter areas. This is in sharp contrast to birds exposed to lower amplitude anthropogenic noise, where the general finding is that birds sing at higher frequencies and faster song rates. Since acoustic signals convey information about identity, motivation and fitness of the signaller, it is unclear whether the change in song parameters at airports affects the efficacy of the songs. To test the biological significance of this seemingly non-adaptive alteration, playbacks were performed using high frequency and low frequency song types on an airport and control population. There was a strong and indiscriminate response to both stimuli in both populations in song, flight and approach parameters, showing that both stimulus types are effective. However, the airport population physically attacked the speaker substantially more (25/33 individuals) than the control population (5/33 individuals). In addition, airport birds attacked the speaker more in response to low frequency stimuli than high frequency stimuli. As high frequencies are typically the first to be lost when hearing is impaired due to acoustic overexposure, these results support recent findings suggesting that birds exposed to frequent, high amplitude noise show symptoms of auditory threshold shifts.

4.1 Introduction

Environmental noise generated by natural events is ubiquitous and selection has worked to maintain optimal signal transmission in noisy habitats (Slabbekoorn & Smith 2002). The modification of acoustic signals in response to anthropogenic noise has been detected in many bird species (Slabbekoorn & Ripmeester 2008). A typical response from birds is that they adjust the spectral frequency of the song or they switch to song types that contain frequencies that are not masked (Slabbekoorn & den Boer-Visser 2006; Brumm 2006a). Many studies investigating the effects of anthropogenic noise on signalling focus on constant, low frequency noise and little is known about how birds respond to acute intermittent high level noise events, such as those generated by aircrafts (however see: Gil et al. 2014; Dominoni et al. 2016). The extreme levels and wide frequency spectrum of aircraft noise is enough to saturate all auditory filters preventing the detection of any sound and yielding complete masking (Moore 2012). Therefore, the changing of spectral structure of acoustic signals would not be an effective strategy near airports.

In many bird species, songs are used by both sexes to assess the singer's quality (Collins 2004; Searcy & Nowicki 2005). Information conveyed within the signal informs the receiver of the sender's reproductive status (Amrhein et al. 2002), motivation to attack (Searcy et al. 2006) and fighting ability (Linhart et al. 2012). For example, spectral frequency is often a reliable indicator of body size and for many species females show preferences for males that produce relatively low frequencies (Pasteau et

al. 2007). Temporal characteristics of signals can be varied to provide information of aggressive intent, with signals being delivered either faster (Linhart et al. 2013) or slower (Ręk & Osiejuk 2010). Complexity of signals is another way of conveying information and is used in both mate selection (Catchpole & Slater 1995) and male-male interactions (Riebel & Slater 2000). Receivers use the information to make a choice of either responding vocally, escalating into a physical encounter or to move away from the signaller (de Kort et al. 2009). Any modification to the structure of a signal that improves transmission may also alter the information encoded within it. Spectral adjustment such as the increase in frequency to improve transmission may be costly in both inter- and intra-sexual interactions, especially in species where females show preferences for lower frequencies (Halfwerk, Bot, et al. 2011).

When noise interferes with signalling, the signal may be detected, but not enough fine scale information is received to allow for signal discrimination (Lohr et al. 2003). In some cases females may lose the preference for particular song characteristics, such as low frequency syllables (Wollerman & Wiley 2002; Aunay et al. 2014). Response to territorial intrusions may be lower in areas affected by anthropogenic noise (Kleist et al. 2016) possibly because signallers are not able to assess the quality of the intruder. In other cases important signals may be masked completely by road noise resulting in no response at all (Grade & Sieving 2016).

Similar to many other bird species, chiffchaffs (*Phylloscopus collybita*), respond to constant, low frequency noise from highway traffic by

increasing the minimum frequency of their songs (Verzijden et al. 2010). This is presumably to increase signal-to-noise ratios and release it, at least partially, from the masking effects of the noise. However, chiffchaffs found around airports do not increase the minimum frequency but rather use lower maximum and peak frequencies than those in quiet areas (See chapter 3). This means that the signal remains within the frequency range of the aircraft noise. An explanation for these apparent non-adaptive findings is the loss of auditory feedback for high frequencies as a consequence of auditory detection threshold shifts (for more details see chapter 3 this thesis).

Delivery rate and spectral characteristics are important parameters in the song of chiffchaffs (Linhart et al. 2012). Any alteration to these parameters may alter the information conveyed within the signal. To identify if the reduction in maximum frequency, as observed in birds living close to an airport, alters the information content natural variation in songs were artificially polarized to contain either a greater proportion of high or low frequency syllables. The signal value of high versus low frequency syllables was tested by observing the responses of male chiffchaffs to simulated territory intrusions containing either a high proportion of high or low frequency syllables. Responses of males around Manchester airport were compared to those in relatively quiet areas. If the alterations to song types observed at airports have a biological significance, birds at the control site would discriminate between the two stimuli types. However, if detection and discrimination thresholds for

airport birds have shifted and high frequency syllables are not detected, responses would differ, as not all of the information within high frequency stimuli would be perceived.

4.2 Methods

Study sites and species

Playback experiments were performed at Manchester airport (53.3593, -2.2706) and Woolston Eyes nature reserve (53.3899,-2.5388). Both sites are characterised by mixed broadleaf woodland and scrubland, with willow (*Salix sp.*), sycamore (*Acer pseudoplatinus*) and oak (*Quercus sp.*) the dominant tree species. The airport site is part of Manchester Airport Groups' environmental mitigation area, and has seen varying levels of land management including woodland translocation, public footpath building and coppicing. Woolston Eyes is a nature reserve located approximately 20km west of the airport. Both sites hold approximately 40-50 singing male chiffchaffs during the peak of the breeding season.

Chiffchaffs are summer migrants to Europe, with the first males usually arriving in March. Males defend their territories by singing from strategic positions throughout the breeding season, which typically concludes at the end of June. Songs rates do not reduce after males secure a mate so are thought to be used primarily in male-male interactions (Rodrigues 1996). Chiffchaffs mediate social interactions between males by modifying temporal and spectral song parameters. Fighting ability is signalled with a relatively low peak frequency (Linhart et al. 2012) whilst increasing the duration of songs signals motivation to fight (Linhart et al. 2013).

Playback procedure

Playback trials were conducted between 0600 and 1100 during a two-week period from to 31st March to the 19th April 2014. Focal birds were followed and GPS location of each singing post was recorded. Territory maps were

built with territories being classified as an area triangulated from a minimum of three singing posts. Once a territory had been defined, a remote controlled speaker (Fox Pro Fury, www.gofoxpro.com) was placed in a tree within the territory at head height (approx. 1.8m). All observations were conducted from a camouflaged pop-up hide positioned approximately 10m from the speaker to reduce the effects of the observer on the response of the subject. Prior to playback, the observer entered the hide and a five-minute habituation period was observed. Trials were abandoned if the subject moved out of sight or interacted with a conspecific. Adjacent territories were not used in the same 24hr period to avoid carryover effects. If territories were within 50m of each other, one of these territories was randomly selected and removed from further analysis, to reduce the risk of sampling an individual twice. To control for confounding effect of seasonality, airport and control sites were visited on alternate days throughout the study period.

Playback design

Playback stimuli were prepared in the same way as described in Linhart *et al.* (2012). Chiffchaff songs around airports have been shown to have lower maximum frequencies than those in quieter areas (Chapter 3). This is a result of airport birds using a higher proportion of a low frequency syllable type (hereafter 'airport type') than control birds. Airport birds were also shown to use a high frequency syllable type significantly less than control birds (hereafter 'control type'). To create 'airport type' stimuli all 'control type' syllables within a song were substituted for 'airport type' (Fig. 4.1 (b)). For control type stimuli, airport type syllables were substituted for the control type (Fig/ 4.1 (c)). Recordings from 22 individuals (n=11 airport site, n=11 control site) were used to generate the stimuli.

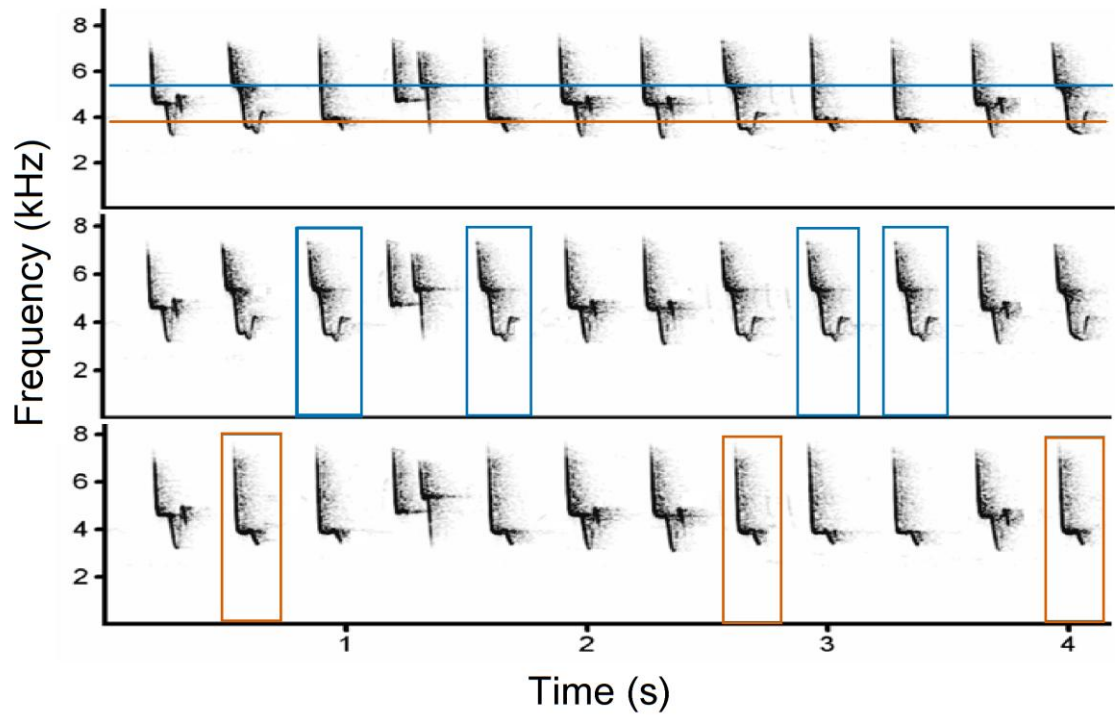


Figure 4.1: Schematic of manipulated chiffchaff (*Phylloscopus collybita*) songs used for testing the signal value between different song types. Spectrograms show a typical chiffchaff song used for manipulation (A); the same song following the replacement of low frequency syllable to create airport type stimuli (B), and the same song with replacement of high frequency syllable types to create control type stimuli. Red boxes indicate where low frequency syllables have been replaced with high frequency syllables. Blue boxes indicate where high frequency syllable types have been replaced with low frequency syllables.

Songs were randomly selected using the sample function with replacement in R (R core team 2016) from a database of recordings made by AW in 2014 (sampling frequency = 44 kHz, WAV format). Only songs that contained both airport type and control type syllables were used for manipulation. Song files were band-pass filtered between 1000-9000hz and normalized to 90% of the maximum amplitude in Avisoft-SASlab (Specht. R, Berlin, Germany). Chiffchaff song duration and rate conveys information about aggressive intent, with faster and longer songs indicating higher levels of aggression (Linhart et al. 2013). To ensure that responses to manipulated songs were not influenced by any alteration in temporal patterns, song duration and syllable rate of manipulated songs were compared between pairs of stimuli. Song lengths and syllable rates of manipulated songs did not differ from the original recordings or

between airport type or control type stimuli (Kruskal Wallis $p > 0.05$). Manipulated songs were tested for differences in maximum, peak and minimum frequency parameters using Wilcoxon-signed ranks tests. Airport songs had significantly higher maximum ($N_1 = 11$, $N_2 = 11$, $W = 437$, $P = 0.003$) and peak frequencies ($N_1 = 11$, $N_2 = 11$, $W = 641$, $P = <0.001$) but there was no significant difference in minimum frequency between stimuli types ($(N_1 = 11$, $N_2 = 11$, $W = 152$, $P = 0.46)$).

Each playback trial was divided into three 120-second observation periods. An initial 'pre-playback' period consisted of 120 seconds of silence and acted as a baseline activity period for that subject. This was followed by two post-playback observation periods consisting of 30 seconds of playback followed by a 90-second observation period for two subsequent stimulus exposures.

Behavioural responses were recorded using a data logging application (SpectatorGo! http://www.biobserve.com/products/spectator_go/) on a touch screen device (iPod touch: www.apple.com). Subject responses were measured by comparing four behavioural variables: (1) attack, the number of times the individual came into physical contact with the speaker, (2) flight rate, the number of times the subject flew over or under the speaker, (3) close approach: time spent within 2 meters of the speaker and (4) song rate, the number of times the subject vocalised during each observation period.

Data analysis

Generalised linear models assuming a Poisson distribution and log link function were built to assess the effect of stimulus type on each of the behavioural responses. Julian date and the site from where the stimulus was recorded (Airport or control) were added as additional independent predictors to investigate effects of seasonality and recording location. Model selection was based on Akaike's Information criteria for each model (Zuur et al. 2009). Following model selection, distributions of the residuals

for the model with the lowest AIC score were inspected to ensure there were no violations of normality or signs of over dispersion. Where necessary, sequential Bonferroni corrections were applied to control for the increased probability of type 1 errors through multiple testing (Rice 1989).

A common mistake when analysing crossover trial data is to not consider carry over effects (Díaz-Uriarte 2002). That is that the response to the second treatment is a continuation of response to the first. To test for cross-over effect, Mann-Whitey U tests comparing number of responses to the first playback to the number of responses to the second playback were used. Wilcoxon signed ranks tests were performed to test for any effect of order, that is response to a stimulus type was not influenced by being played first or second. Non-parametric tests were used as all variables violated assumptions of normality (Shapiro-Wilks test for normality- All variables: $P = >0.05$).

4.3 Results

Airport site

Attack rate

The model with the lowest AIC value contained only the variable stimulus type. There was a significant increase in number of attacks following exposure to Airport type stimuli compared to pre-playback ($n=33$, $Z = 3.44$, $p = 0.001$), but there was no significant response to the control type ($n=33$, $Z = 0.95$, $p = 0.35$). There was a significant difference between number of attacks depending on stimuli type (Control type vs Airport type; $Z = 2.49$, $p = 0.03$)

Flight rate

The model with all terms (Stimulus type, Julian date and recording location) had the lowest AIC value. There was no effect of stimulus type or recording location on flight rate (p values all > 0.05). Date however had a significant effect with birds flying less as the season progressed independent of which stimulus was played ($n = 33$, $Z = -1.96$, $p = 0.04$).

Approach rate

The model with the lowest AIC value contained only the variable stimulus type. Both stimuli elicited a significant response (Airport type stimuli; $n=33$, $Z = 3.25$, $p = 0.001$; control type, $n=33$, $Z = 4.97$, $p = <0.001$). There was no significant difference between approach depending on stimulus type (Control type vs Airport type; $Z = -1.72$, $p = 0.18$).

Song rate

The model with the lowest AIC value contained the variables stimulus type and Julian date. Both stimulus types elicited a significant reduction in the number of songs produced (Control stimulus: $n=33$, $Z = -4.64$, $p = <0.001$; Airport type: $n=33$, $Z = -4.83$, $p = <0.001$). However, a post hoc Tukey test showed no difference in singing response between the two stimuli (Control type vs Airport type; $Z = -0.13$, $p = 0.99$). There was also a significant negative effect of Julian date on song with birds singing less

following playback as the season progressed ($n = 33$, $Z = -3.41$, $p = <0.001$).

Control site

Attack rate

The model with the lowest AIC value contained the variables stimulus type and recording location. There was no significant effect of either variable on the number of attack responses (all p values >0.05).

Flight rate

The model with the lowest AIC value contained the variables stimulus type and Julian date. Julian date had a significant negative effect on flight with birds responding less as the season advanced ($n = 33$, $Z = -5.17$, $p = <0.01$). Stimulus type had no significant effect on flight response (all p values > 0.05).

Approach rate

The model with the lowest AIC value contained only the variable stimulus type. Birds approached the speaker more in response to both the Airport ($n=33$, $t = 2.09$, $p = 0.001$) and control type stimuli ($n=33$, $t = 3.57$, $p = <0.001$). There were no significant difference in time spent within two metres of the speaker between stimuli types (Control type vs Airport type; $Z = -1.48$, $p = 0.30$).

Song rate

The model with the lowest AIC value contained only the variable stimulus type. There was a significant negative response to both playback stimuli (Airport type: $n=33$, $t = -1.072$, $p = 0.006$; Control type: $n=33$, $t = -3.097$, $p = 0.002$). There was no significant difference in response between stimulus types ($n = 33$, $Z = -2.064$, $p = 0.9$).

Table 4.1 Model selection results exploring the response of male chiffchaffs (*Phylloscopus collybita*) to playbacks containing either a higher number of high or low frequency syllables. Birds were either holding territories around Manchester airport or a control site (see text). For each model the number of estimated parameters (K), Akaike's information criterion values (AIC) and differences in AIC (ΔAIC)

	K	AIC	ΔAIC
Airport			
Attack rate			
Stimuli type	3	127.8182	-
Stimuli type + recording location	4	129.3018	1.4836
Stimuli type + Date	4	129.6757	1.8575
Stimuli type + Date + Recording location	5	131.2753	3.4571
Recording location	2	167.9654	40.1472
Date	2	168.3393	40.5211
Date + recording location	3	169.9389	42.1207
Flight rate			
Stimuli type + Date + Recording location	5	168.141	-
Stimuli type + Date	4	169.3407	1.1997
Stimuli type + recording location	4	170.0852	1.9442
Stimuli type	3	174.1079	5.9669
Date + recording location	3	220.2276	52.0866
Date	2	221.4273	53.2863
Recording location	2	222.1718	54.0308
Approach rate			
Stimuli type	5	2132.217	-
Stimuli type + Date	4	2134.432	2.215
Stimuli type + Date + Recording location	3	2181.058	48.841
Stimuli type + recording location	4	2183.051	50.834
Date + recording location	3	3655.439	1523.222
Date	2	3657.654	1525.437
Recording location	2	3706.273	1574.056
Song rate			
Stimuli type + Date	5	360.6663	-
Stimuli type + Date + Recording location	4	362.8883	2.222
Stimuli type	3	372.6528	11.9865
Stimuli type + recording location	4	373.7288	13.0625
Date + recording location	3	388.854	28.1877
Date	2	391.076	30.4097
Recording location	2	401.9166	41.2503

	K	AIC	ΔAIC
Control			
Attack rate			
Stimuli type + recording location	4	61.39488	-
Stimuli type + Date + Recording location	5	62.95034	1.55546
Stimuli type	3	66.39252	4.99764
Stimuli type+ Date	4	68.26635	6.87147
Recording location	2	71.13329	9.73841
Date + recording location	3	72.68874	11.29386
Date	2	78.00476	16.60988
Flight rate			
Stimuli type + Date	4	137.8137	-
Stimuli type + Date + Recording location	5	139.4973	1.6836
Stimuli type	3	163.7696	25.9559
Stimuli type + recording location	4	165.3712	27.5575
Date	2	174.837	37.0233
Date + recording location	3	176.5206	38.7069
Recording location	2	202.3946	64.5809
Approach rate			
Stimuli type	5	1542.775	-
Stimuli type + Date	4	1542.903	0.128
Stimuli type + Date + Recording location	3	1548.576	5.801
Stimuli type + recording location	4	1549.214	6.439
Date + recording location	3	2246.255	703.48
Date	2	2246.383	703.608
Recording location	2	2252.694	709.919
Song rate			
Stimuli type	3	425.9588	-
Stimuli type + Date	4	426.2116	0.2528
Stimuli type + Date + Recording location	5	427.0184	1.0596
Stimuli type + recording location	4	427.0319	1.0731
Date	2	435.4109	9.4521
Date + recording location	3	436.2178	10.259
Recording location	2	436.2312	10.2724

Carry over and order effects

A total of 33 playback trials were conducted (Airport: n=33, control: n=33). No carry over effects (MWU test all variables $p > 0.05$) or effects of playback order (Wilcoxon signed ranks test all variables $p > 0.05$) were detected for any of the response variables.

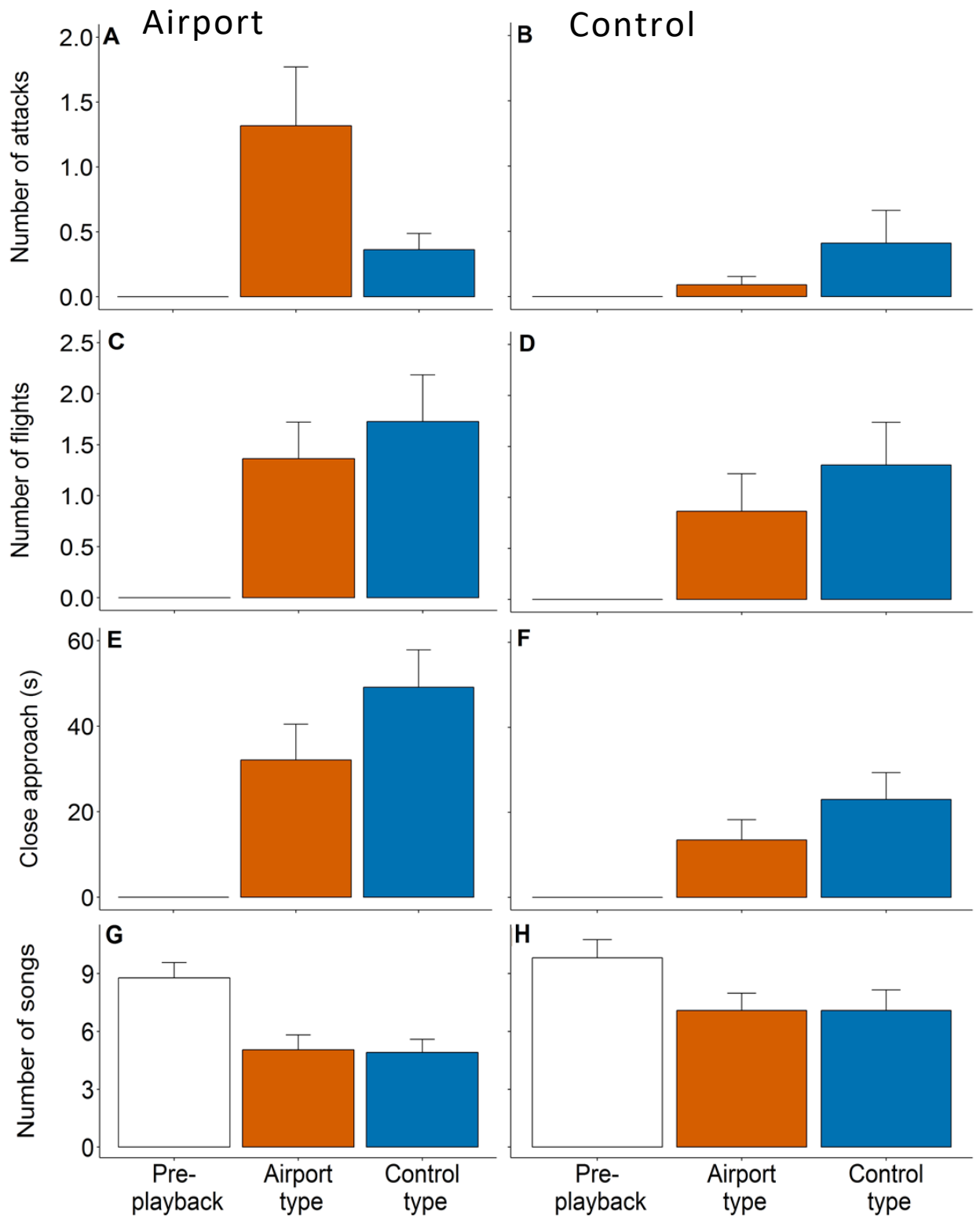


Figure 4.2: Responses of male chiffchaffs (*Phylloscopus collybita*) holding territories around Manchester airport (A, C, E, G) and control sites (B, D, F, H) to playbacks of modified conspecific songs. Response parameters are: (1) attack, the number of times the individual came into physical contact with the speaker, (2) flight rate, the number of times the subject flew over or under the speaker, (3) close approach, time spent within 2 meters of the speaker and (4) song rate, the number of times the subject vocalised during each observation period. X-axis categories: Pre playback = Observations recorded during 2 minute period before exposure to stimuli, airport type = observations following exposure to songs containing syllables used by birds near the airport; Control type = observations following exposure to manipulated songs containing syllables used predominately by birds in quiet areas.

4.4 Discussion

The results suggest that high frequency syllables are perceived differently, or not at all by airport birds, possibly as a result of noise induced hearing loss (See chapter 3 this thesis). Chiffchaffs living close to an airport physically attacked the speaker 5 times more in response to a simulated territory intrusion than those in control areas. The chiffchaffs exposed regularly to aircraft noise also attacked the speaker more often in response to stimuli with a relatively high proportion of low frequency syllables. Control birds did respond to both stimuli but did not show a difference in attack response between the stimulus types. Similarly to previous song manipulation playback experiments on chiffchaffs, no difference in any other response parameters were found between stimuli (Linhart et al. 2013). .

Chiffchaffs show a presumed non-adaptive alteration to their song when exposed to high amplitude, aircraft noise by singing slower songs with predominantly lower frequency syllables (Chapter 3 in this thesis). This contrasts with the usual findings that birds increase the spectral frequency and delivery rate of their songs in response to anthropogenic noise, presumably to increase signal-to-noise ratios (SNR). The use of lower frequencies is interpreted as non-adaptive here as the modified songs remain within the frequency range of the noise. Whilst this contradicts signal adjustment to improve SNR, however similar song type changes do take place in birds that are hearing impaired (see chapter 3 this thesis).

In the case of Noise Induced Hearing Loss, higher frequency elements are typically the first to be lost (Holme & Steel 2004). If Chiffchaffs exposed to aircraft noise are suffering from auditory threshold shifts and are no longer able to detect higher frequencies, the response to songs with a high proportion of high frequencies would differ to responses to songs with more low frequency syllables. Indeed, the results here show that high

frequency song types elicited significantly fewer attacks than low frequency song types in the airport population.

There are two main reasons why these findings support auditory threshold detection shifts. Firstly, chiffchaffs are more likely to attack if the frequency of the intruder's song is higher than their own (Linhart et al. 2012), presumably because they interpret relatively higher frequencies as being produced by a lower quality individual (de Kort et al. 2009). Birds exchange singing bouts to assess each other's motivation and fighting prowess (Vehrencamp et al. 2013). However, if a low quality individual enters the territory this ritual can be foregone and an immediate attack ensued. As airport chiffchaffs use lower frequency songs than birds in quiet areas (Wolfenden *et al.* in prep), a stronger response to high frequency songs should be expected rather than the weaker response reported here. Therefore, the lower number of attacks to the high frequency stimuli may be because noise induced hearing loss caused by aircraft noise impairs the detection of all of the information within the intruder's song. This would mean that not enough information is received by the territory holder to assess the quality of the intruder.

Secondly, syllable rate is a reliable indicator of aggressive intent in chiffchaffs (Linhart et al. 2012). The stimuli that each chiffchaff received were identical, in terms of duration and syllable rate. In the case of the control birds, there was no difference in response between stimuli suggesting that both stimuli have the same signal value. Airport birds however physically attacked the speaker more in response to low frequency stimuli. An explanation for this is that if high frequency syllables within a song are not completely heard, airport birds may not receive enough information to trigger an aggressive response. Decreased aggression to high frequency songs is interpreted here as a result of a decline in perception of information encoded within the signal.

Song alteration to increase signal transmission affects intra-sexual communication by altering response intensity in blackbirds (*Turdus merula*) (Ripmeester et al. 2010) and Great tits (*Parus major*) (Mockford & Marshall 2009). However, no difference in response was detected in male Australian magpies (*Cracticus tibicen*) response to songs recorded from noisy and quiet populations (Potvin et al. 2013). There is limited evidence for how noise induced signal alteration modifies inter-sexual responses. However, changes of frequency parameters can weaken female preferences (Halfwerk, Bot, et al. 2011; Aunay et al. 2014). I show here that males respond differently to conspecific songs that differ in frequency parameters, presumably as a result of auditory detection threshold shifts. In many cases, the trait used to convey aggression is shared with those used in mate selection (reviewed in Wong & Candolin 2005). Therefore, the findings reported here may not just reveal the impacts of aircraft noise on male-male interactions, but also reflect the potential influence on mate selection.

Finally, an interesting observation is the level of aggression observed from airport birds. In humans, exposure to loud anthropogenic noise causes annoyance (Basner et al. 2014). This annoyance can be the result of the noise disrupting daily activities or if the noise affects communication (Clark & Stansfeld 2007). Annoyance in humans can lead to increases in stress levels and subsequent reductions in quality of life through reduced immune response (Clark & Stansfeld 2007). The increased levels of aggression observed from Chiffchaffs around the airport may be due to an increased level of annoyance. This in turn could increase stress levels and have further implications on reproductive success and disease resistance (Kight & Swaddle 2011).

Conclusions

Results from this study support previous findings that chiffchaffs found around Manchester airport suffer from noise induced hearing loss. These results also show airport birds are more aggressive than birds in quieter areas. With the development of air transport links globally, the number of animals exposed to extreme noise levels will increase. Understanding how animals respond both behaviourally and physiologically will allow us to predict the impact of such developments and allow the development of mitigation strategies.

Chapter 5: No effect of aircraft noise on corticosterone levels in nestling blue tits

Abstract: Anthropogenic noise generated by roads, urban areas and industry negatively influences population dynamics, species diversity and vocal communication in birds. Exposure to anthropogenic noise can also lead to changes in the concentrations of the glucocorticoid-corticosterone. Glucocorticoids are hormones responsible for directing resources towards behavioural or physiological actions that increase chances of survival during stressful situations. Because corticosterone levels are often higher following a stressful event, they are used as a proxy to assess stress. There are conflicting results showing either positive, negative or no effects of continuous road noise on the corticosterone levels in developing chicks. However, the effect of intermittent aircraft noise on chick development is not known. Intermittent noise has a stronger effect on physiological and behavioural responses in birds. Here the impacts of exposure to continuous and intermittent noise on circulating corticosterone levels are compared for 11 -day old blue tit chicks (*Cyanistes caeruleus*). To exclude potentially confounding effects of environmental or genetic factors on corticosterone levels, a two-way cross-fostering design was used. Overall, blue tit chicks showed no significant corticosterone response following exposure to synthetic road or aircraft noise, nor was there any effect of cross-fostering. These results suggest that neither intermittent nor continuous noise is perceived as stressful by blue tit chicks. Given that blue tits are ubiquitous in urban areas, these findings may provide some insight to why the species is able to tolerate city life.

5.1 Introduction

Anthropogenic noise influences avian ecology by affecting species distributions (McClure et al. 2013) and modifying community compositions (Francis et al. 2009). The impact of anthropogenic noise appears to be species specific with some species being more sensitive to noise disturbance than other closely related species (Francis et al. 2011a). Noise exposure also leads to negative physiological responses. This includes damage to the hearing apparatus in birds (Dooling & Popper 2007) and fish, increases in physical deformities in marine larvae (de Soto et al. 2013), reduced testosterone levels in mice (Ruffoli et al. 2006) and a lower immune response (Kight & Swaddle 2011). Therefore, it may be said that life in a noisy environment is stressful.

Quantifying stress in free ranging animals can be difficult. Elevated glucocorticoid levels are often used as a proxy for assessing chronic stress in birds (Angelier & Wingfield 2012). When a bird encounters a stressful situation, the hypothalamus-pituitary-axis (HPA) is stimulated and glucocorticoids are secreted. Corticosterone (hereafter CORT, a glucocorticoid) plays an integral role in restoring homeostasis in birds by redirecting internal resources towards self-maintenance processes (Angelier et al. 2015). These changes include reduction in appetite, increased blood flow leading to faster cognitive processing and activation of the immune system (Sapolsky et al. 2000). CORT concentrations are a good indication of stress levels experienced by an individual as they reflect the amount required to maintain homeostasis.

Many species, including humans (Spreng 2004), show elevated glucocorticoids when exposed to noise. Sage grouse (*Centrocercus urophasianus*) show lower occupancy at leks when exposed to playbacks of road noise, and males that remain at the leks have elevated CORT levels (Blickley & Patricelli 2012). Long-term effects of elevated CORT levels include decreased health (Saino et al. 2002), lower survival rates (Blas et

al. 2007) and reduced song output (Macdougall-Shackleton et al. 2009). Elevated CORT levels are also associated with changes in behaviour. Chickens (*Gallus domesticus*) exposed to long periods of noise in the form of loud music show not only increased levels of CORT but are also more fearful (Campo et al. 2005).

The effects of Increased CORT levels are not necessarily negative (Crino & Breuner 2015). White crowned sparrow (*Zonotrichia leucophrys*) chicks living near roads showed increased CORT levels. However chicks with high CORT levels were significantly larger, a reliable proxy for higher fitness, than those in quiet areas (Crino et al. 2011). Adult male Zebra finches (*Taeniopygia guttata*) with high CORT levels show faster problem solving skills (Crino et al. 2014) and have greater reproductive success (Crino et al. 2014).

Most studies on noise-induced stress focus on adult responses. The limited experimental evidence on the impact of noise on developing birds shows conflicting and surprising results. House sparrow chicks (*Passer domesticus*) exposed to playbacks of road noise showed no difference in CORT levels compared to chicks in quiet areas (Angelier et al. 2015). White crowned sparrow chicks have lower CORT after exposure to road noise (Crino et al. 2013). Both of these studies investigated the impact of continuous noise, similar to that generated around urban areas or road networks. Possible explanations for these results are that the focal species are less sensitive to noise disturbance (Schwabl 1999) or that the development of hearing in altricial chicks is delayed (Kubke & Carr 2000). Sage grouse attendance at breeding sites is affected more by intermittent than continuous noise (Blickley et al. 2012), possibly because it is more difficult to habituate to. Experimental exposure to intermittent chronic noise leads to lower growth rates compared to control groups in developing chickens (Voslarova et al. 2011). For birds living close to airports, noise exposure consists of relative quiet periods, punctuated by

frequent bouts of high amplitude, broad spectrum noise (See Chapter 2). For birds that live within 1km of an airport, the noise levels generated by low altitude aircraft movements frequently exceed 90 dB(A).

The current study aimed to test the CORT response of nestling blue tit chicks to playbacks of two types of anthropogenic noise. Playback experiments allow the separation of noise effects from other possible anthropogenic factors that could increase CORT concentrations. Baseline corticosterone levels of chicks in control nest boxes were compared to chicks exposed to either constant road noise or intermittent aircraft noise. If elevated sound levels act as an environmental stressor on developing chicks, CORT levels would be higher in birds exposed to noisy conditions. As intermittent noise has been shown to be more stressful than constant noise, the prediction is that exposure to intermittent noise would lead to a stronger endocrine response. Finally, variation in CORT levels at 11 days old were compared to the weight of chicks prior to fledging to assess if CORT levels are reliable predictors of fitness.

5.2 Methods

Study site and species

Data were collected during the 2015 breeding season. For this study, a nest box population of blue tits was used located on the grounds of Lancaster University, UK (54°0'N, 02°47'W). The blue tit is a small, abundant passerine distributed throughout Europe and Northern Africa. The species naturally nests in tree cavities, however also readily uses wooden nest boxes. The study site consists of mixed broadleaf woodland with oak (*Quercus* Sp.) and sycamore (*Acer* Sp.) being the dominant species. Within the woodland 111 nest boxes are positioned approximately 10m apart (see Mainwaring et al. 2008, for a detailed description of the site). From the 1st April, all boxes were checked bi-weekly to monitor

occupation. Once new nest construction had been observed, daily checks were undertaken to monitor egg-laying dates.

Experimental design

To reduce potentially confounding environmental or genetic factors that may influence stress responses, a balanced, two-way cross-fostering experimental design was used. Each experimental dyad consisted of two nest boxes, with each box containing chicks from both nests (Fig. 5.1). Chicks were cross-fostered two days after hatching of the first egg. Clutches were only considered for fostering when eggs in both boxes

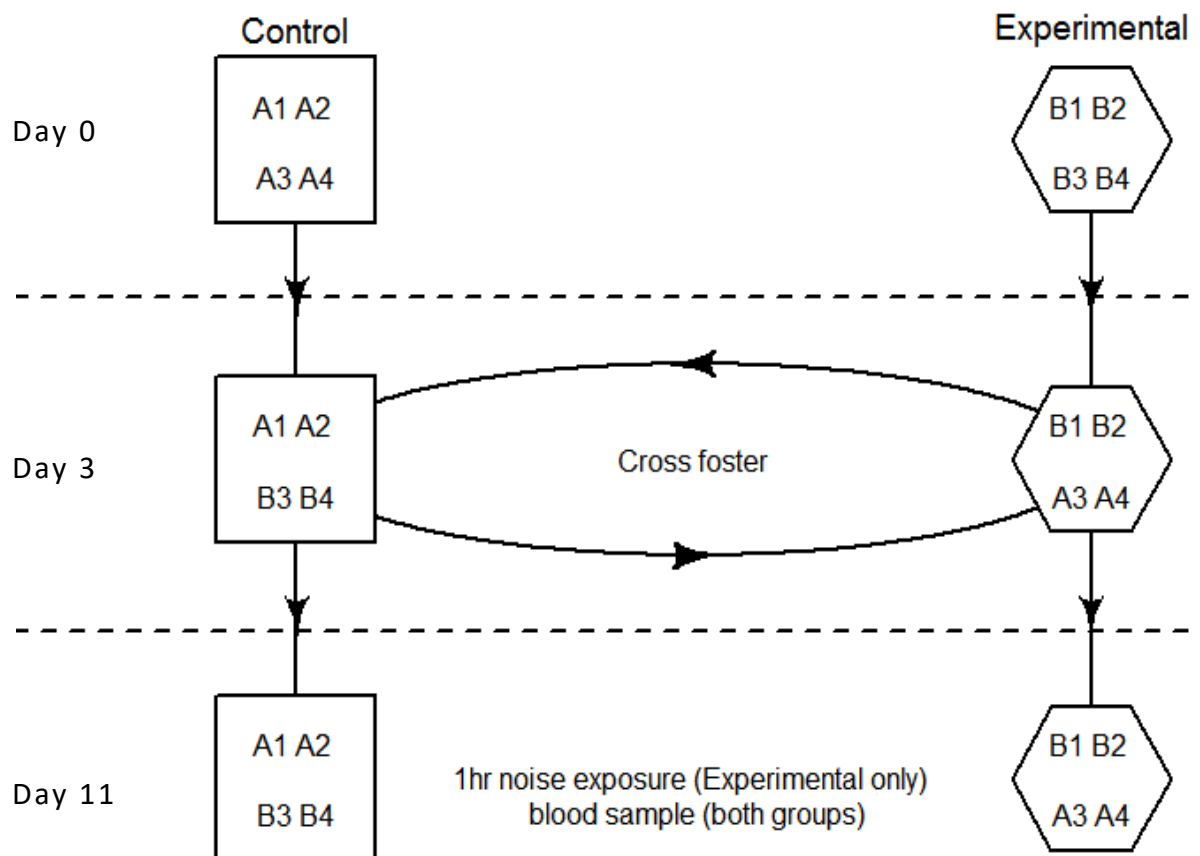


Figure 5.1: Schematic overview showing the experimental procedure for assessing the effects of noise on 11 day old nestling blue tits (*Cyanistes caeruleus*). An experimental dyad comprised of pairs of boxes that contained chicks from both nests. Square boxes represent the control nest boxes, hexagonal boxes represent experimental nest boxes. Experimental nest boxes were presented with a 1hr recording of either continuous noise or intermittent noise replicating exposure to either road noise or aircraft noise. Day 0 indicates the day the first egg within a dyad hatched. Pairs of nest boxes where the first egg hatched on the same day were used for cross fostering.

hatched on the same day. The number of chicks fostered was equal between boxes and was half of the brood in the box with the smallest number of chicks. All chicks within a nest box were marked by clipping the tip of a toenail on either the left or right foot. As an additional visual aid for separation of home and fostered chicks, numbered British Trust for Ornithology (BTO) metal rings were fitted two days prior to sampling to either all fostered or non-fostered chicks in a box. Prior to cross fostering all chicks within a nest were weighed to the nearest 0.01g using an electric balance (Pesola MS500; www.pesola.com). Only chicks of similar weight ($\pm 0.5\text{g}$) were candidates for fostering. All chicks were weighed 14 days after hatching to obtain weights prior to fledging.

Playback procedure

Speaker inserts were positioned on top of the nest boxes on both experimental and control nest boxes approximately 20 weeks prior to the beginning of the breeding season (c.f. Halfwerk et al. 2011; 2016). The inserts consisted of wooden boxes (dimensions 16cm(W) x 12cm(D) x 20cm(H); Fig.5.2) that replaced the original nest box lid. Stimuli were presented for one hour prior to blood sampling. Stimuli were played via an external MP3 player (Hama DP-200, <https://www.hama.com>) hidden in the undergrowth at the base of the nest tree and connected to a full-range speaker (Peerless 2.5 inch, 10-10,000Hz, 1 watt). Playback stimuli were divided into two treatment types: (1) road noise- continuous synthetic noise and, (2) aircraft noise- intermittent synthetic noise. Road noise files were created by band-pass filtering a one-hour sample of white noise between 1-10Khz (Halfwerk & Slabbekoorn 2009). Noise generated by aircraft movements follow a quadratic distribution with amplitude increasing to a peak before tailing off as the plane moves away. Therefore, aircraft noise files were created by bandpass filtering white noise (1-10 KHz) that matched the noise profile of actual aircraft movements with a ramp-up leading to a peak amplitude, followed by a ramp-down. Stimuli

were created in Adobe Audition (www.adobe.com). Aircraft stimuli replicated the number, duration and frequency of actual aircraft movements from Manchester Airport. This was determined by inspecting 1-hour long recordings taken between 0700 and 1200, from five different days. Aircraft recordings were obtained using a Songmeter (Wildlife acoustics) placed 200m away from the runways. For both treatment types maximum amplitude levels were set at 65 dB(A) 30cm from the speaker cone (measured with a Cassella CEL-246 sound level meter, A-weighted, fast response). This simulated the average noise exposure levels in natural nest cavities around Manchester international airport (AW pers. Obs.). Playback was started via the MP3 player placed at the base of the nest tree. Each playback started with 10 minutes of silence before the noise started to limit the impact of observer presence.



Figure 5.2: Image of nestbox with speaker insert used to test effects of anthropogenic noise on developing blue tit chicks (*Cyanistes caeruleus*) (c.f. Halfwerk et al. 2011; 2016). 1-hour long playbacks of artificial aircraft or road noise were presented to 11-day old chicks. Corticosterone concentrations extracted from blood samples were compared between treatment boxes and boxes that received no noise exposure.

Sample collection

Following the end of the playback stimuli, all chicks were removed from the nest box and placed on heat pads. Time from the end of the playback to chicks being removed did not exceed 5 minutes for any of the treatment boxes. Using the leg ring identifiers, two 'home' chicks and two 'fostered' chicks were randomly selected and placed in individual containers. 30-40 microlitres of blood was taken from the brachial vein by Ian Hartley. As CORT levels in birds can be influenced by handling (Müller et al. 2006), the time from removal from the nest to blood being taken was recorded to test for the effects of handling stress. Blood samples for all chicks were taken within 4 minutes of being removed from the nest. Control blood samples were collected identically to experimental birds. To ensure variation in CORT could not be due to circadian rhythm (Romero & Remage-Healey 2000), all samples were collected between 0800 and 1000. Samples were stored in a cool bag with ice packs until transfer to the lab. Samples were spun in a centrifuge for 10 minutes at 15,000rpm. Plasma was separated from the red blood cells using a micropipette and stored in 3ml plastic vials before transfer to a freezer (-20°C). All samples were spun, separated and placed in the freezer within 60 minutes of collection.

Corticosterone concentrations were extracted using an established radioimmunoassay procedure (Pottinger & Carrick 2001). Ethyl acetate was added to plasma samples (1:10; plasma: ethyl acetate) and following centrifugation, 50µl of the extract was transferred to assay tubes (hereafter referred to as unknown concentrations). To enable levels of unknown concentrations to be calculated, standard curves of 'known' concentrations were created using assay tubes containing known inert cortisol concentrations ranging from 800 to 6.25 picograms. Blank assay tubes contained only ethyl acetate. The solvent was then extracted from both 'known' and 'unknown' assay tubes under a vacuum oven at 40°C. 200µl of assay buffer containing antibody followed by 25µl of ³H-

corticosterone working solution was added to each of the 'known' and 'unknown' tubes and were incubated at 4°C for 12 hours. Following incubation 100µl of dextran coated charcoal (DCC) was added into each tube. Tubes containing DCC were vortex mixed and incubated on ice for 5 minutes. Following incubation, samples were placed in a centrifuge and spun at 2,500 rpm for four minutes at 4°C. 150µl of the solution was then added to 4ml of scintillant, mixed by inversion and counted under standard tritium conditions for 5 minutes. A 3-parameter hyperbolic decay function was applied from the known concentrations using the percentage of corticosterone solution bound against the inert cortisol. This curve was then used to derive the concentration of corticosterone in the 'unknown' plasma samples.

Statistical analysis

CORT levels within each treatment group violated assumptions of normality (Shapiro-Wilk's test; Control: N =47, W = 0.87, P = <0.001; Road: N =23, W = 0.75, P = <0.001; Plane: N = 19, W = 0.65, P = <0.001) so non-parametric tests were used. To assess if CORT levels were influenced by handling stress, a Kruskal-Wallis test was used to identify if handling times differed between nest boxes. Secondly, a Kruskal-Wallis test was used to assess if CORT levels differed based on the order of chick sampled. A Pearson's correlation test was performed to explore correlations between handling time and CORT levels.

Generalised linear mixed effect models are often used on data where repeated measures are taken for each experimental unit (Bolker et al. 2009). Whilst there were repeated measures for each nest box within this experiment, replications were too few for mixed effect models to be appropriate (Bolker et al. 2009). To identify if CORT levels varied between control and treatment types generalized linear models (GLM) were built using the lme function in statistics software R (R core team, 2016). Brood type (cross fostered or not) and brood size (the number of chicks in the

same nest box) were added as additional terms. Models were first built assuming a Poisson distribution; however, on inspection of the distribution of the residuals, over-dispersion was apparent. Models were then built using a quasi-Poisson distribution, post-hoc inspection of residuals showed no issues of homoscedasticity or over-dispersion.

Because the sample sizes were small, an additional analysis was conducted by combining the aircraft and motorway noise samples. Generalised linear models assuming Poisson distributions were used to test for CORT variation between control and noise nest boxes and to explore interactions between home and fostered chicks.

In addition to exploring the CORT response of chicks within each dyad, stress response was also explored between chicks from the same box and compared to levels in chicks from the same dyad. If the response to a stressor has a genetic component, CORT levels between chicks from the same box should show the same trend. Given the limited number of replicates (2 sample units per box), no statistical analysis were performed however a summary of the findings and scatterplots of CORT levels were inspected for signs of relationships.

Finally, to identify if stress levels could influence development of chicks, GLM's were used to explore if CORT level at 11 days old was related to the mass of chicks close to fledging.

Model selection for all analysis was determined using Akaike information criteria (AIC) (Zuur et al. 2009). The distributions of the residuals for the models with the lowest AIC score were inspected to ensure there were no violations of test assumptions. All statistical analyses were performed using R (R core team 2016)

5.3 Results

Sample sizes and handling stress

Between 16th and 30th April 2015, 88 out of 111 nest boxes were occupied by breeding pairs (79.28%). Of the 88 boxes with eggs, 54 pairs were cross fostered resulting in 27 experimental dyads. Prior to any other manipulation 15 of these dyads (55%) failed because of either partial or total loss of chicks from one of the nest boxes. Of the remaining 34 boxes not cross fostered or manipulated in any way for this experiment 23 (68%) failed by means of total loss of all chicks. 100% of the chicks that had blood sampled successfully fledged. Chick losses were attributed to extremely low temperatures and heavy rain resulting in lack of invertebrate food items.

Plasma samples were obtained from a total of 94 chicks from 12 dyads (Aircraft dyads; N = 6, Road dyads; N = 6). Five samples were removed because volumes were too small (n=1) or because CORT concentrations could not be detected (N=4) yielding a final sample size of 89. Due to the small volumes of blood collected, plasma volumes ranged between 25 and 50µl. Time taken to obtain blood samples from chicks did not differ between boxes ($\chi^2 = 20.77$, df = 22, P = 0.53). There was no effect of order of chicks sampled on CORT levels ($\chi^2 = 4.94$, df = 3, P = 0.29) and no relationship between CORT levels and handling time (r= 0.17, t= 1.25, p = 0.22).

CORT response

Mean CORT level (\pm standard deviation) for chicks from the control group was 2.51 ± 2.37 (N = 47), for the aircraft noise group it was 3.36 ± 3.80 (N = 19) and for the road noise group it was 2.40 ± 3.35 (N = 23, Fig. 3).

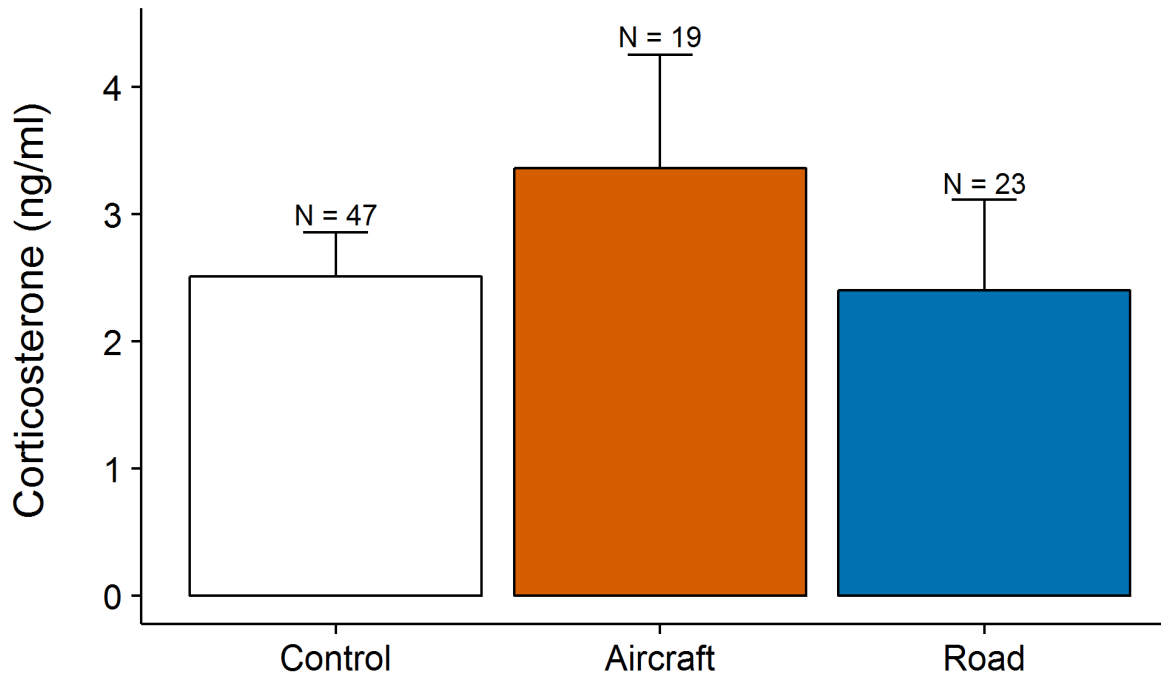


Figure 5.3. Mean (\pm S.E.M) corticosterone levels of 11-day old blue tit chicks (*Cyanistes caeruleus*) exposed to 1 hour of intermittent noise (Aircraft), continuous noise (Road) or no noise (control). All corticosterone concentrations were obtained from blood samples collected within 4 minutes of chicks being removed from the nest.

The null model containing all explanatory variables (CORT level, brood type and brood size) fitted the data best. The removal of any independent variable or their interactions did not improve the fit (all IV combinations $P > 0.05$). There was no significant effect of stimulus type on CORT levels (CORT~Road: $N_{\text{control}} = 47$, $N_{\text{Road}} = 23$, $t = -0.73$, $p = 0.47$; CORT~Plane: $N_{\text{control}} = 47$, $N_{\text{Airport}} = 19$, $t = -0.08$, $p = 0.93$). There were also no effects of cross fostering (cort~brood type; $N_{\text{home}} = 45$, $N_{\text{Away}} = 44$, $t = 1.16$, $P = 0.39$).

There was no significant CORT response when data for the two stimuli were combined into a general noise category ($N_{\text{control}} = 47$, $N_{\text{Noise}} = 42$, $t = 0.38$, $P = 0.15$) but there was a non-significant trend for cross-fostered chicks to have higher CORT levels than non-cross-fostered chicks ($N_{\text{home}} = 45$, $N_{\text{Away}} = 44$, $t = 0.6$, $P = 0.08$).

CORT levels within the same box vary both within treatments and between siblings. However, in 7 of the 22 boxes (B5, B9, 42, A15, A8 and 90) variation in CORT levels between siblings was similar despite some related individuals being in a different box and receiving a different treatment (Fig. 5.4).

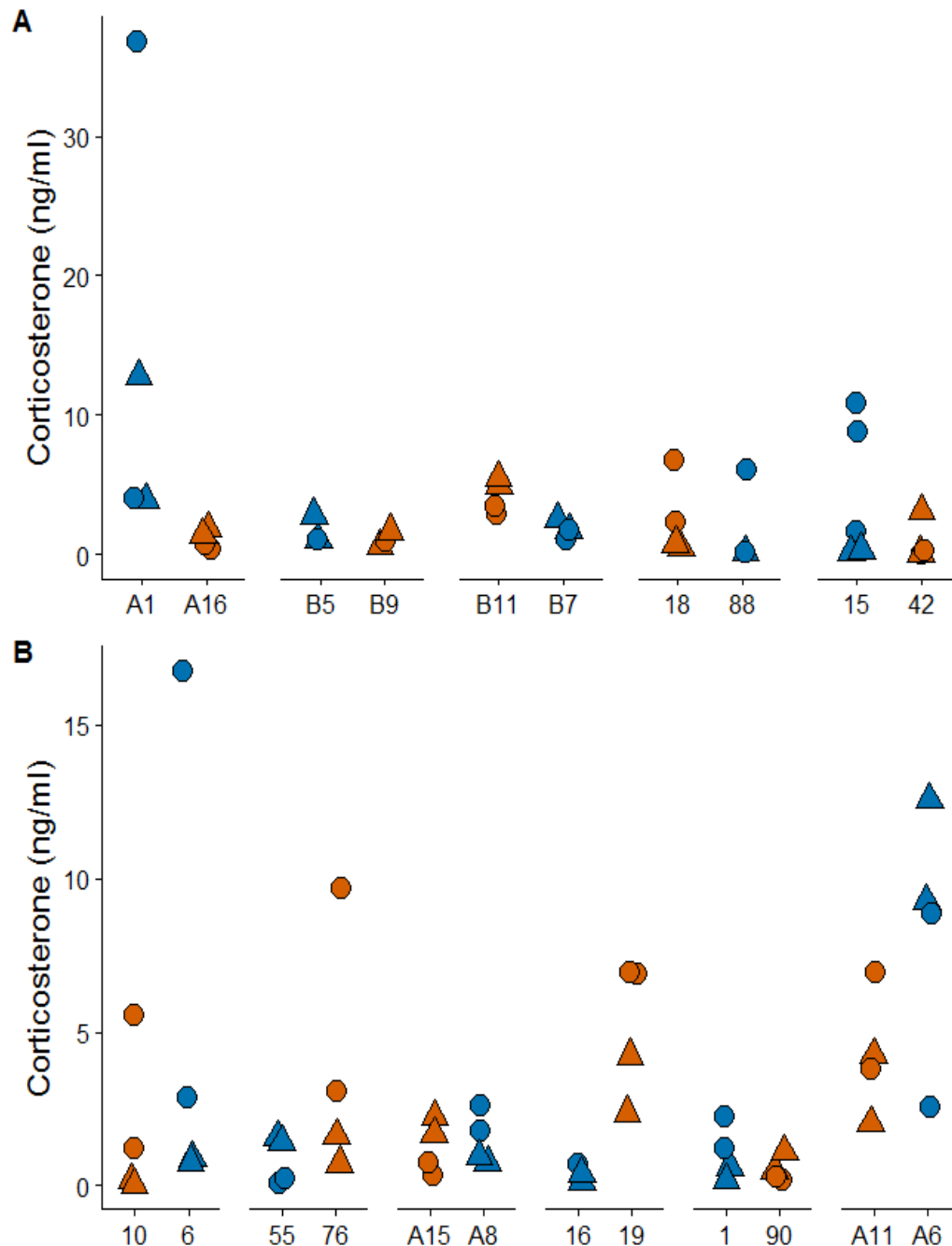


Figure 5.4. Comparison of corticosterone levels within and between 11 day old blue tit chicks (*Cyanistes caeruleus*) (N= 89). Points in the same plot window indicate chicks from the same experimental dyad. Colours indicate if the chick was in a box that received a playback stimulus (red) or in a control box (blue). Shape indicates if it was cross fostered (triangle) or reared in the box it was born in (circle).

Effects of CORT on body mass

Weights of chicks at 14 days old varied between 8.8g and 13.5g with a mean weight of 10.85 ± 0.85 . There were no effects of CORT levels on chick weight at 14 days old (Cort~body mass; $N = 89$, $t = 1.51$, $P = 0.14$; Fig. 5)

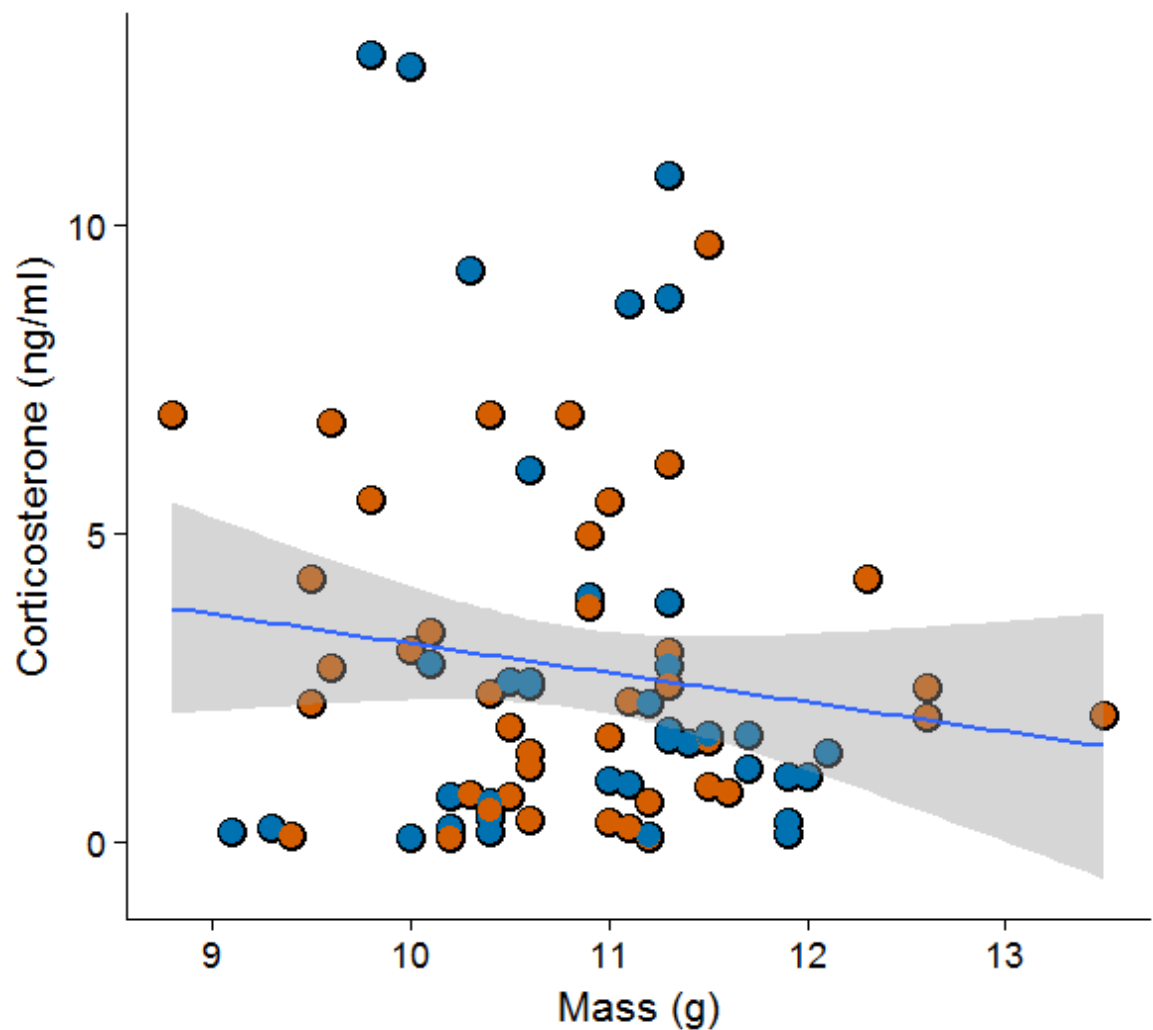


Figure 5.5. Corticosterone levels of 11 day old blue tit chicks (*Cyanistes caeruleus*) and weight at 14 days old ($N = 89$). Red circles indicate chicks that received 1-hour exposure to either aircraft or road noise. Blue circles indicate control chicks.

5.4 Discussion

Eleven-day old blue tit chicks were exposed to either a 1-hour recording of continuous artificial road noise or a 1-hour recording that simulated multiple aircraft movements. Based on CORT levels, there was no evidence to support the hypothesis that aircraft noise is an environmental stressor to blue tit chicks. In addition, there were also no differences in CORT levels between control chicks and chicks exposed to road noise. Whilst no previous data were available on how chicks respond to intermittent noise disturbance, these findings are consistent with previous results in nestling birds that also report CORT levels were unaffected following exposure to a constant noise source (Crino et al. 2013, Angelier et al. 2016).

An explanation for the apparent lack of stress response is that young chicks do not perceive noise as a stressor as the brain and adrenal functions are not yet fully developed. Similarly to hearing, there is evidence that the development of the HPA-axis is slower in altricial birds than in precocial birds (Schwabl 1999). Precocial mallards (*Anas platyrhynchos*) and domestic chickens (*Gallus domesticus*) show peaks in corticosterone prior to hatching and newly hatched chicks show an increase in corticosterone as a result of handling stress (Holmes et al. 1992). This suggests that for some precocial birds, the HPA-axis is functional prior to hatching. However, for many altricial species HPA activity increases with age. Serins (*Serinus serinus*), an altricial species, have lower CORT levels in response to handling stress at 5 days old compared to 12 days old (Schwabl 1999). Delayed maturation of the HPA-axis is thought to be adaptive and reduces the negative effects that elevated CORT levels can have on growth and development (Sapolsky 1986). The lack of response reported here might be due to the immaturity of the chicks. As many altricial birds show adult-like stress responses prior to fledging (Schwabl 1999), repeating this experiment on older chicks or

measuring CORT levels in incubating females may provide a clearer representation of the effects of noise exposure on birds.

A second potential explanation is that as a species, blue tits are resilient to environmental stressors. Anthropogenic disturbance, including noise can lead to a filtering effect on the presence of certain species, leading to reduced species diversity (Francis, Ortega, et al. 2011b). What species are affected by noise appears to correlate with the frequency of the vocalisation they use (Francis, Ortega, et al. 2011b), with species using low frequencies more affected. However having high frequency songs alone may not be enough to succeed in noisy environments (Moiron et al. 2015). Certain bird species may be better suited to life in urban areas, due to physiological, behavioural or dietary factors (Croci et al. 2008). These so called 'Urban exploiters' possess combinations of specific traits that may allow them to adapt to novel environments (Croci et al. 2008). These traits include reproductive factors such as nest type, providing high levels of parental care and nesting date. Non-reproductive traits typical of urban exploiters include flexible feeding strategies and sociality (Croci et al. 2008). Blue tits are ubiquitous in urban areas and their distribution appears to be relatively unaffected by acute aircraft noise (see thesis chapter 2). As with blue tits, house sparrow chicks, another successful urban species, show no corticosterone response when exposed to continuous noise (Meillère et al. 2015). The lack of HPA activity in response to either intermittent or constant noise indicates that the species do not perceive noise as an environmental stressor. This lack of stress response to anthropogenic noise may be a factor in the species' capabilities to prosper in noisy, urban areas.

Finally, the lack of CORT response may be due to a natural reduction of the hormone. The intensity of CORT response is positively correlated with the perceived threat level (Angelier 2015). A peak in CORT concentrations will be detected in response to a threat. Cort concentrations will reduce over

time if the threat level decreases. Therefore the lack of CORT response detected here may be as a result of the birds habituating to the 1hr long noise stimuli.

Conclusions

Here, no effects of anthropogenic noise on stress response were detected in blue tit chicks. However, the lack of stress response observed in chicks may not fully reflect the physiological impact of prolonged exposure to acute noise. Further work including measuring corticosterone in adult birds exposed to aircraft noise or similar experimental work on species not found in urban areas would provide more information of the physiological consequences of living close to airports. Finally, experiments that expose individuals to varying amplitudes would also inform of the physiological effects of acute intermittent noise on corticosterone levels.

Chapter 6: The impact of aircraft noise on distribution, communication and physiology of birds

6.1 Introduction

The aim of this PhD research was to assess the impact of aircraft noise on vocal communication and species composition of bird species around Manchester international airport.

To fulfil this aim, four objectives were addressed: (1) the effects of aircraft noise on the avian community or how noise influences bird species diversity, abundance and density. The effects of aircraft noise on acoustic communication from the perspective of (2) the signal sender and (3) the signal receiver. Finally (4), to investigate the impact of aircraft noise on stress hormone response in developing chicks. Combined these four objectives provide detailed information on the impacts of aircraft noise on life history traits of birds.

6.2 Community effects

Chapter 2 of this thesis found that some bird species that were present in quiet sites were not observed in noisy areas. There was however no evidence for an effect of noise on woodland bird species diversity (Chapter 2). Results of community assessments derived from point count also revealed no differences in community composition. Finally, the density of the five most abundant bird species did not vary with increasing noise levels. These findings provide the first evidence that noise generated by aircraft movements from Manchester airport does not affect woodland bird diversity. Whilst the data provide a strong case study, the data incorporate only a single airport and a single habitat type. Further work that encompasses a variety of habitat types and extends to a number of airports would provide data to support and allow generalisation of the current findings.

The Manchester Airport Group (MAG) has invested heavily in environmental mitigation to offset the loss of habitat following the construction of the second runway in 1997. This includes the generation of new areas of scrubland and the regeneration of multi-species grassland habitats. The substantial mitigation effort and the generation of suitable habitats conducted by the airport may go some way in explaining why the number of woodland bird species were similar near to and further away from the airport.

However, the results reported may not fully describe the impact of aircraft noise on the bird community. The presence of a species does not necessarily mean that there is no impact (discussed in chapter 2). Anthropogenic noise not only affects bird communities by reducing diversity but also modifies population demographics. Proportionally higher numbers of immature birds are present in areas affected by road noise (Mcclure et al. 2016) and industrial noise (Habib et al. 2006). Data on population demographics were not collected during this study. However,

further work around airports using mist netting and colour banding would allow data to be collected on age demographics, assess territory sizes and monitor the movements of individuals. These data would provide more detailed information on how resident and migratory bird species respond to aircraft noise.

As well as modifying population demographics, the effects of noise extend to influencing reproductive success. These influences can be either positive, with a decrease in nest predation (Francis, Paritsis, et al. 2011) or negative, with fewer eggs produced (Kight et al. 2012) and increases in embryo mortality (Potvin & MacDougall-Shackleton 2015). The introduction of nest boxes in suitable habitat around the airport would allow the reproductive success and thus fitness of some bird species to be monitored.

6.3 Communication effects

Signallers

Chapter 3 showed that chiffchaffs (*Phylloscopus collybita*) around airports use lower maximum frequencies and sing songs at slower rates than birds from a control population. This finding was replicated in two airports and two control sites in two countries. The findings contradict many other studies on noise related signal adjustment in birds that typically show an increase in spectral frequency (Brumm 2006a; Slabbekoorn 2013) and an increase in delivery rate (Brumm & Slater 2006; Brumm et al. 2009). Explanations for these findings are that the adjustment is not a result of selection for improved signal to noise ratio, but rather it results from noise induced hearing loss (NIHL). Whilst evidence from the literature is provided that show the noise levels generated by aircraft are high enough and at a broad enough frequency spectrum to support this claim, additional data is required to provide conclusive evidence.

Evidence in support of the argument for NIHL could be provided by two primary sources. Firstly, hearing loss can be determined in birds by examining the condition of the hair cells in the inner ear (Dooling et al. 1997). The examination of the hearing apparatus of birds from a range of species resident around airports would show signs of damage to the hair cells. As birds are able to recover hearing by regenerating the hair cells within the ear within approximately 10 days following exposure (Dooling et al. 1997), samples from resident birds would be required. As some of the larger resident bird species are actively culled around airports to maintain aircraft safety (corvids, raptors). Samples from multiple species for multiple airports may be obtained quickly and without the need for potentially controversial collection. By not only using a number of airports but also a range of species, species specific variations in cell damage would be highlighted and, if some species are more prone to NIHL than other, may help to explain why some birds are absent from noisy sites.

Secondly, behavioural feedback experiments such as Go-No-Go experiments allow data to be collected on the hearing ability of individual birds (Dooling et al. 1997). These types of experiments allow audiograms to be constructed for individuals that inform of the ability to detect signals at varying amplitudes. Comparing audiograms before and after experimentally exposing subjects to aircraft noise could be used to identify changes in hearing sensitivities at different frequencies.

Receivers

Chapter 2 argues that modifications to temporal and spectral song parameters in chiffchaffs is an artefact of noise induced hearing loss. Chapter 3 took this a step further by testing the receiver's perception of songs that contained either a higher proportion of high or low frequency syllables. The ability to detect high frequencies is usually the first to be lost as a result of noise induced hearing loss. The response of signal receivers to high and low frequency song types was compared in

individuals around Manchester airport and a control population. Overall, airport birds physically attacked the playback speaker 5 times more often than control birds, showing that they are substantially more aggressive. Speculative explanations for these findings may be that, similarly to humans (Clark & Stansfeld 2007), aircraft noise is perceived as an annoyance and therefore the tolerance levels of the birds are lower. Increases in annoyance levels in humans have positive correlations with increases in symptoms of stress related illnesses such as hypertension and cardiovascular disease (Clark & Stansfeld 2007). Tolerance levels may also be affected due to disturbance in sleep patterns. Humans exposed to road and aircraft noise show not only increased aggression but also have reduced cognitive function and lower immune responses (Pepper et al. 2003). As discussed in chapter 1, distraction by noise can result in slower response time to an external stimulus that could lead to an increased risk of attack by a predator. Therefore, birds found around airports may not only be hearing impaired and more aggressive they may also be unhealthier and at a greater risk of predation.

The results of the playback experiment also show that there was a higher level of aggression in response to the lower frequency song type. This suggests the songs are perceived differently and is likely to be a result of not being able to detect high frequencies. Chapter 4 focused on the differences in response of birds to different types of territorial song. There are however other important vocal signals that may be affected by shifts in auditory detection thresholds. Alarm calls are used by birds to alert others around them to the threat of a predator (Evans et al. 1993). If birds around airports are suffering from noise induced hearing loss, important signals necessary for survival may not be perceived. Further work comparing the response of a range of bird species to playbacks of alarm calls would provide further information on the cost of living close to an airport.

6.4 Physiological effects

Chapter 5 showed that repeated exposure to aircraft noise did not lead to increased levels of circulating stress hormone, corticosterone. This study provides the first data suggesting that intermittent noise is not stressful to developing chicks. These results are consistent with studies using continuous noise that show no effect of exposure on the corticosterone levels in chicks (Crino et al. 2013; Angelier et al. 2015). There were also no effects of noise on the growth of chicks with no significant variation in pre-fledging mass detected between treatment and control birds. An explanation for why no corticosterone response was observed in the blue tits (*Cyanistes caeruleus*) in this study and also in the species used in previous experiments is that the endocrine system may not be fully developed (see chapter 5). A repeat of this experiment but instead measuring corticosterone levels in adult birds, or in species where chicks have fully functioning endocrine systems may provide more conclusive evidence that aircraft noise is perceived by birds as an environmental stressor.

As negative behavioural responses to noise are highly species specific (Conomy et al. 1998), the same may be true for the magnitude of physiological response. Extensions of this experiment may include a range of species, both common and absent from noisy areas, to aircraft noise to identify if some species show higher physiological responses to noise disturbance than others.

Personality or sex specific sensitivities may also play some part in variations in response to noise. Great tits (*Parus major*) that show strong negative responses to novel objects and exhibit slower exploratory behaviours are affected more by noise than more bold individuals (Naguib et al. 2013). Although quantifying personality traits in free-living conditions is difficult, assessing the personality phenotypes of birds found

around airports would provide information on if airport birds are bolder than those found in quieter sites.

6.5 Future plans

As discussed in chapter 1, low frequency noise attenuates less than high frequency and therefore travels over larger distances. This is because long frequency wavelengths are less affected by reverberation or absorption than high frequency wavelengths (Berglund et al. 1996). Indeed, low frequency noise generated by aircrafts can still be detected 5000km away from the source (Liszka 1978). Whilst this figure is impressive, the effects of inaudible, low frequency noise may be greater still. Inaudible noises for humans can be either those with frequencies greater than 20,000 Hz (ultrasound) or those with frequencies below 20Hz (infrasound). Natural sources of ultrasound are rare but they are used by several mammal species in echolocation. Infrasound is much more common and can be caused by weather conditions such as wind and thunderstorms. Infrasound is also used by many animals for communication, for example African elephants (*Loxodonta Africana*) (Langbauer 2000) use infrasound to signal to conspecifics and male peacocks (*Pavo cristatus*) use infrasound during courtship rituals (Freeman & Hare 2015).

Infrasound not intended for communication can also trigger a response in wildlife. Alterations to migration routes of golden winged warblers (*Vermivora chrysoptera*) are correlated to infrasound caused by a hurricane 900km away (Streby et al. 2015). Experimental exposure to infrasound generated by piston movement changes migration routes in European eels (*Anguilla Anguilla*) (Sand et al. 2000) .

Infrasound levels generated by aircraft are much louder than those audible to the human ear (Rubin 2005). This is important to animals living in areas close to airports as damage to the hearing cells can still take place, even if the noise is not heard (Berglund et al. 1996). This and many

other studies principally investigate the effects of dB(A) levels on wildlife. The A-weighted decibel scale does not include frequencies that are outside of the frequency range of humans. A-weighted measurements therefore do not detect infrasound. As infrasound is louder than the audible noise generated by aircraft engines and that infrasound has a negative effect on birds it is recommended that future studies should focus on using un-weighted (dB(Z)) noise levels (Fig. 1).

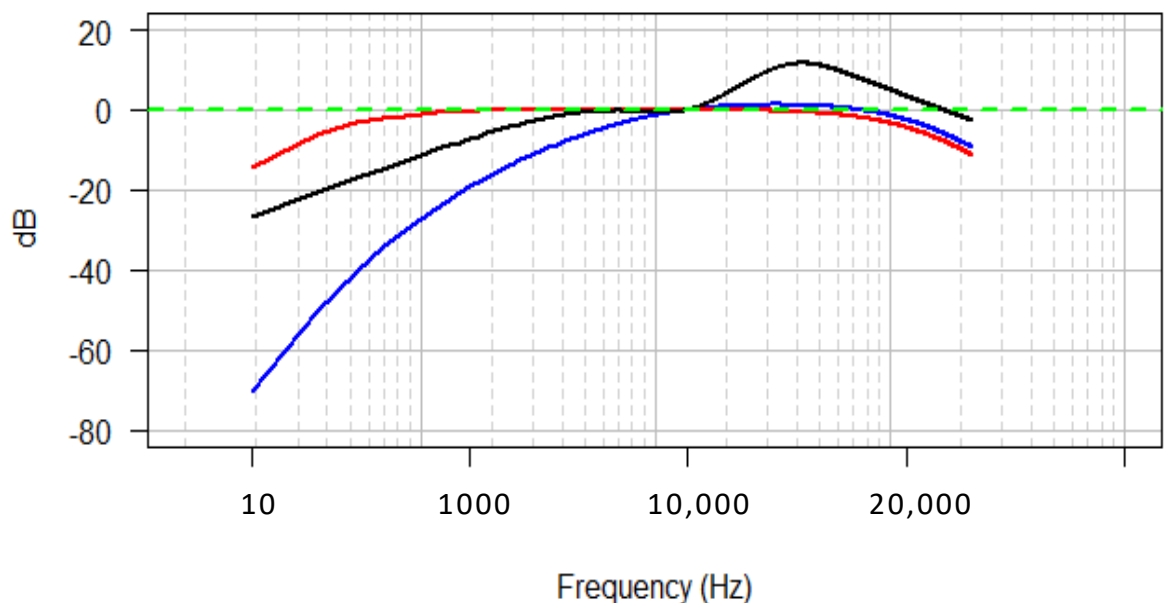


Figure 1: Sensitivities of frequencies for different decibel weightings. Weightings sensitive to frequencies detected by humans and birds dB(A) is indicated by the blue line. Measures weighted to include low frequency noise dB(C) and dB(D) are indicated with the red and black lines respectively. Un-weighted decibel level (dB(Z)) is indicated with the dashed green line.

Whilst this study aimed to investigate how aircraft noise affected the distribution and communication of birds, it generated questions on how noise affects the hearing of wildlife exposed to frequent aircraft movements. The number of aircraft movements and associated noise levels are sufficient to cause temporary and permanent threshold shifts (discussed in chapter 1). The habitat of the non-operational areas around Manchester airport is predominately improved grassland and is leased to

farmers for grazing livestock. This provides a unique opportunity to obtain data to assess the impact of aircraft noise on domestic animals. Behavioural observations of livestock could inform of any influence of noise on social dynamics. In addition, samples of the auditory apparatus could be obtained from the animals following slaughter to assess if aircraft noise affects causes hearing loss in mammals living close to the airport.

This PhD showed that aircraft noise affects the song and the perception of song in birds. The most likely explanation for this is as a result of noise induced hearing loss. This is the first study to provide evidence that anthropogenic noise alters detection thresholds in free living birds. Although this work focused on a single species, the results can very likely be generalised to other wildlife. Although there was limited evidence that birds avoid living near aircraft noise, there is likely to be a fitness cost to those that do.

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Appeddix 1: Summary of habitat variables and results for comparison between point count locations for assessing the impact of aircraft noise on avian species abundance.

Point count ID	location	Tree height	Canopy cover	Tree density	Tree species
1	Rossmill wood	11	87	9	3
2	Rossmill wood	12	96	9	7
3	Rossmill wood	8	95	9	6
4	Rossmill wood	9	90	6	7
5	Rossmill wood	10	91	3	5
6	Rossmill wood	10	85	7	5
7	Rossmill wood	9	88	10	6
8	Rossmill wood	9	89	9	8
9	Sunbank wood	12	94	9	6
10	Sunbank wood	12	94	10	7
11	Sunbank wood	12	85	9	8
12	Sunbank wood	8	97	8	6
13	Sunbank wood	12	93	10	2
14	Sunbank wood	8	97	7	5
15	Sunbank wood	12	85	8	3
16	Sunbank wood	10	94	4	8
17	Runway 1	8	93	9	5
18	Runway 1	8	86	7	6
19	Runway 1	12	91	6	3
20	Runway 1	8	98	9	8
21	Runway 1	10	91	6	8
22	Runway 2	12	92	7	8
23	Runway 2	8	96	7	5
24	Runway 2	11	89	6	8
25	Runway 2	11	98	6	7
26	Runway 2	12	87	7	5
27	Runway 2	9	86	10	5
28	Quarry bank mill	12	95	5	3
29	Quarry bank mill	9	98	10	6
30	Quarry bank mill	10	100	9	8
31	Quarry bank mill	8	87	7	5

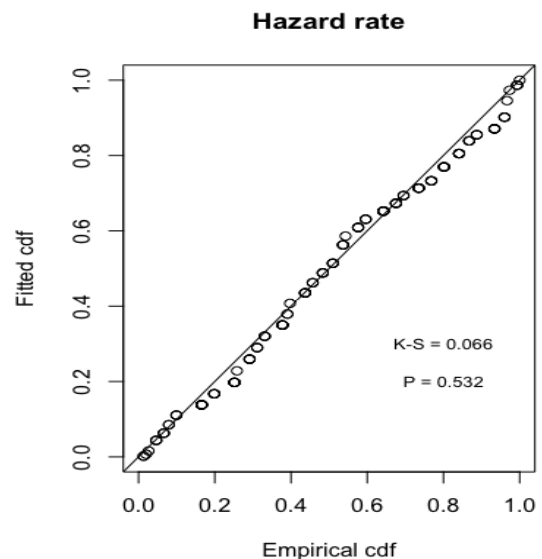
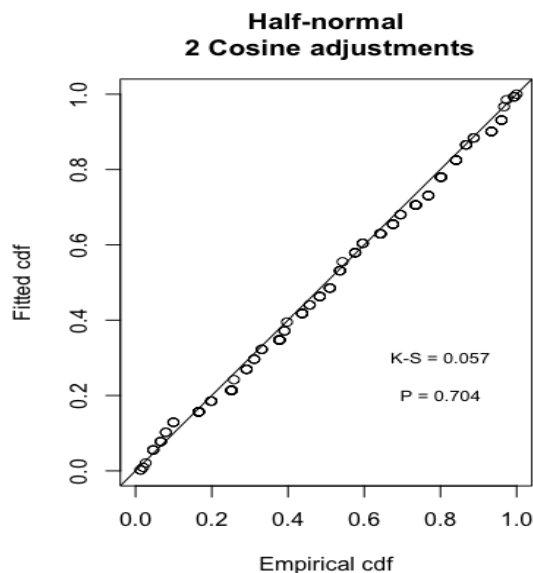
32	Quarry bank mill	11	95	6	8
33	Quarry bank mill	12	98	10	4
34	Quarry bank mill	8	96	7	8
35	Quarry bank mill	10	96	6	8
Kruska-Wallis chi-square		3.6	6.83	3.76	2.87
Degrees of freedom		4	4	4	4
P-Value		0.463	0.145	0.436	0.58

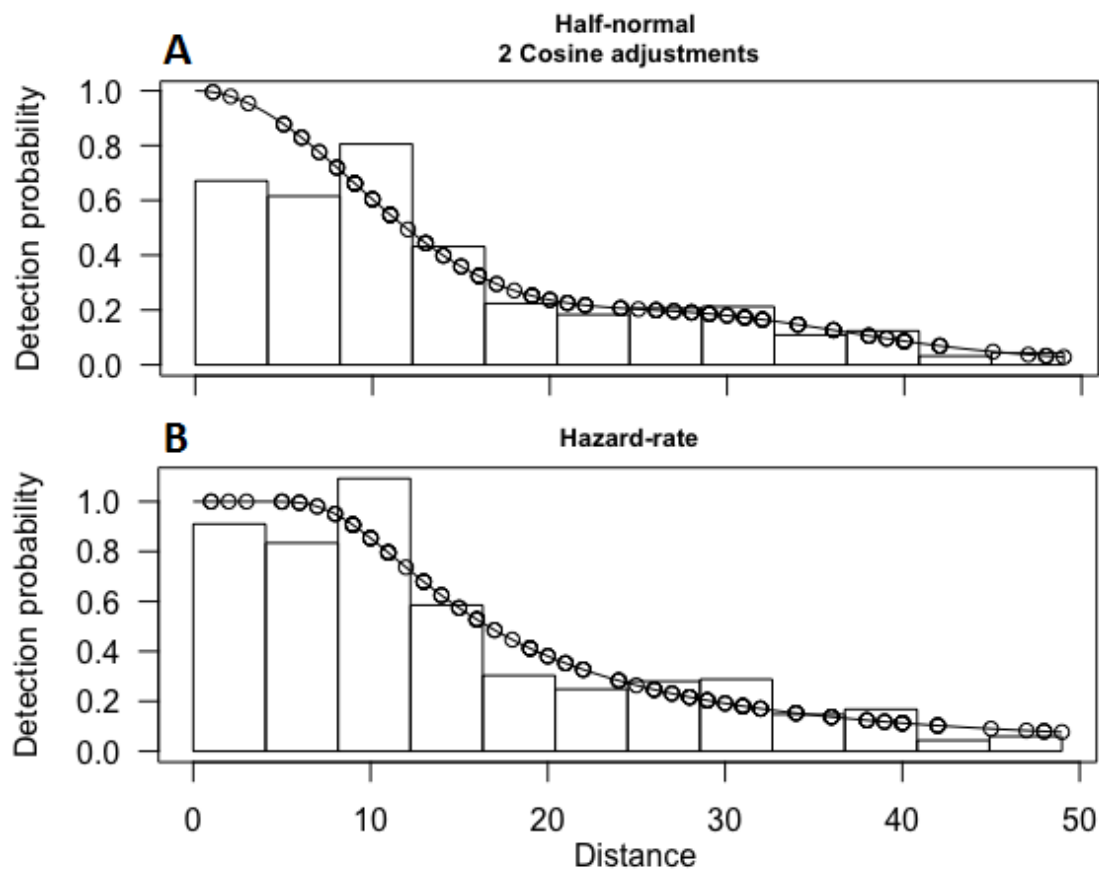
Appendix 2: Total number of species detected during point counts around Manchester airport. Columns indicate the number of detections for each species from point counts exposed to aircraft noise between 50-60dB(A), 60-70 dB(A) and over 70 dB(A).

Species	Scientific name	50-60	60 - 70	>70	Species total
Wren	<i>Troglodytes troglodytes</i>	23	17	15	55
Robin	<i>Erithacus rubecula</i>	22	13	12	47
Blackbird	<i>Turdus merula</i>	14	13	14	41
Blackcap	<i>Sylvia atricapilla</i>	9	10	12	31
Blue tit	<i>Cyanistes caeruleus</i>	11	9	10	30
Great tit	<i>Parus major</i>	12	6	6	24
Wood pigeon	<i>Columba palumbus</i>	8	7	4	19
Chiffchaff	<i>Phylloscopus collybita</i>	5	7	6	18
Goldcrest	<i>Regulus regulus</i>	11	4	3	18
Nuthatch	<i>Sitta europaea</i>	7	4	5	16
Chaffinch	<i>Fringilla coelebs</i>	4	7	3	14
Song thrush	<i>Turdus philomelos</i>	7	4	2	13
Greater spotted woodpecker	<i>Dendrocopos major</i>	6	2	2	10
Long-tailed tit	<i>Aegithalos caudatus</i>	1	3	6	10
Tree creeper	<i>Certhia familiaris</i>	6	3	1	10
Magpie	<i>Pica pica</i>	3	3	3	9
Stock dove	<i>Columba oenas</i>	4	2	0	6
Carrion crow	<i>Corvus corone</i>	2	3	0	5
Jackdaw	<i>Corvus monedula</i>	3	1	0	4
Jay	<i>Garrulus glandarius</i>	2	2	0	4
Mistle thrush	<i>Turdus viscivorus</i>	1	2	1	4
Bullfinch	<i>Pyrrhula pyrrhula</i>	0	0	2	2
Dunnock	<i>Prunella modularis</i>	1	1	0	2
Buzzard	<i>Buteo buteo</i>	0	1	0	1
Goldfinch	<i>Carduelis carduelis</i>	0	0	1	1
					131

Appeddix 3a: Summary of key models for modelling the abundance and distribution of wrens (*Troglodytes troglodytes*) around Manchester airport. adjustment series, Akaikes information croterain (AIC), differences in AIC and goodness of fit tests including shapiro-Wilks test for normality. As the difference between the top two models is less than 2, histograms display the top two Detection curves: (A) Half normal with 2 cosine adjustments and (B) Hazard rate with no adjustment.

Key function	Adjustment	AIC	ΔAIC
Half-normal	2 Cosine adjustments	1159.557	0
Hazard rate	NA	1161.401	1.844
Hazard rate	2 simple polynomial adjustments	1162.044	2.487
Hazard rate	2 Hermite polynomial adjustments	1162.415	2.858
Half-normal	NA	1162.999	3.442
Hazard rate	2 Cosine adjustments	1163.401	3.844
Uniform	NA	1164.135	4.578
Uniform	2 Cosine adjustments	1164.48	4.923
Half-normal	2 Hermite polynomial adjustments	1164.813	5.256
Half-normal	2 simple polynomial adjustments	1164.999	5.442
Uniform	2 Hermite polynomial adjustments	1172.389	12.832
Uniform	2 simple polynomial adjustments	1181.65	22.093





Appeddix 3a: Summary of key models for modelling the abundance and distribution of robins (*Erithacus rubecula*) around Manchester aiport. adjustment series, Akaikes information croterain (AIC), differences in AIC and goodness of fit tests including shapiro-Wilks test for normality. As the difference between AIC for the top models is close to 2, histograms display the top two Detection curves: (A) Hazard rate with no adjustments and (B) Uniform rate with no adjustment. Hazard rates with adjustments are not shown as detection cures are identical between no adjustment, simple polynomial and hermite polynomial.

Key function	Adjustment	AIC	Δ AIC
Hazard rate	NA	789.378	0
Hazard rate	2 simple polynomial adjustments	789.378	0
Hazard rate	2 Cosine adjustments	791.388	2.02
Hazard rate	2 Hermite polynomial adjustments	791.388	2.02
Uniform	2 Cosine adjustments	791.608	2.23
Half-normal	2 Cosine adjustments	792.193	2.815
Half-normal	3 Cosine adjustments	793.887	4.509
Half-normal	NA	795.978	6.6
Half-normal	2 Hermite polynomial adjustments	797.564	8.186
Half-normal	2 simple polynomial adjustments	797.978	8.6
Uniform	NA	802.95	13.572
Uniform	2 Hermite polynomial adjustments	824.929	35.551
Uniform	2 simple polynomial adjustments	839.787	50.409

